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THE SHAPE OF THE SKELETAL ELEMENTS IN THE HEAD OF A GENERALIZED HAPLOCHROMIS SPECIES: H. ELEGANS TREWAVAS 1933 (PISCES, CICHLIDAE)

With two examples of trophically correlated shape-differences

by

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SUMMARY

The present paper is the first publication in a series dealing with current investigations on the comparative functional morphology of various *Haplochromis* species. The paper deals mainly with the shape-description of the primary skeletal elements in the head of *H. elegans*, a generalized insectivorous *Haplochromis* from the East-African Lakes George and Edward. A primary skeletal element is defined as the largest skeletal unit whose shape is taken to be unchangeable over the period of observation and within the limits of observational techniques. The shape-description concentrates on the topological definition of features relevant to comparative functional morphology of *Haplochromis* species (*e.g.* crests, processes, articulation facets). To avoid ambiguity, the essential topological and directional terms are used in a restricted sense, defined in the section on morphological terms. A so-called "relative reference grid" is defined for each element. Positions and directions in the shape-description of an element always refer to its relative reference grid. In this way the shape-description of an element becomes independent of its positions in the head. An element-bound reference grid is necessary for the quantitative comparison of corresponding elements from different specimens.

The aim of the present paper is to provide a set of nomenclatorial tools to be used for tracing, describing and measuring functional relevant shape-differences in the skeletal elements of *Haplochromis* species. It is hoped that the two examples in the section on trophically correlated shape-differences will demonstrate the applicability of this idea. One example deals with the characteristic shape of pharyngobranchial 3,4 in intrapharyngeal mollusc-crushers, the other example concerns the typical shape of the palatine region in paedophagous *Haplochromis* species.

CONTENTS

* It is with deep regret that we record the unexpeted death at the age of 50 years of Nico Teegelaar a few weeks before this paper was published. The drawings in this work represent his last major contribution to his long series of unique biological illustrations.

INTRODUCTION

With its more than 300 closely related species covering a wide range of adaptations, the genus *Haplochromis* exceeds by far the classical example of adaptive radiation provided by the thirteen species of Darwin's finches. Except for a very few species, all *Haplochromis* are endemic in African lakes and rivers. As holds for the Geospizinae from the Galapagos isles, an ancestral-like type of *Haplochromis* is available and the evolutionary history of this genus is relatively well understood. The range of adaptive radiation of *Haplochromis* is best demonstrated in the trophic specializations and the concomitant differentation in cranial morphology. Among others, trophic types of *Haplochromis* comprise: algal grazers, piscivores, intrapharyngeal mollusc-crushers, insectivores, paedophages and species feeding on benthic crustaceans. Some species are ambivalent in their food-preference. The best known example concerns the transition from one diet to another in insectivorous-molluscivorous species from Lake Victoria. The transition occurs intraspecifically as well as interspecifically (GREENWOOD, 1960, 1974; GREENWOOD & BAREL, to be published).

From the foregoing it will be evident that *Haplochromis* provides an ideal object for comparative studies. Current investigations in the morphology section of our laboratory deal with the comparative

functional morphology of *Haplochromis* species from Lake George and Lake Victoria. The species-flocks from these two lakes are well documented in GREENWOOD's revisions of the Lake Victoria and Lake George *Haplochromis*. (For a summary of these papers, the reader is referred to GREENWOOD, 1974). The revisions are not restricted to taxonomic descriptions but include many data on the ecology, gross anatomy and food-preferences of the species. For none of the other lakes such consistent and comprehensive information is available for *Haplochromis*. Ecological and trophic data are crucial for the student of functional morphology as they provide him with a key to the functional demands (*sensu* DULLEMEIJER, 1974) with which the animal has to cope under natural conditions. Beside these ecological and trophic data, the actual choice of the species to be studied is also influenced by GREENWOOD's observations on the relation between food-preference and trends in gross anatomy. An efficacious selection from the nearly two hundred *Haplochromis* species occurring in Lake George and Lake Victoria, would have been next to impossible without such information.

Morphological differences between the *Haplochromis* species are small and intraspecific variability is relatively high. The feasibility of screening the relations between form and function in these morphologically nearly identical species was greatly advanced by the ideas and the technique developed by ANKER (1974) for the study of the stickleback. His detailed reconstruction from serial-sections of the muscle-skeleton-ligament system led him to intriguing hypotheses about the kinetic possibilities in the fish-head and about the mechanical significance of the histological variety observed in the serial sections. The study on the stickleback's head demonstrates cogently that refined anatomy is a fruitful base for functional morphology. The possibility of checking the general validity of ANKER's hypotheses quantitatively, certainly is a major argument to investigate *Haplochromis* species.

The main part of the present paper describes the shape of isolated skeletal elements from the head of *Haplochromis elegans*, a small insectivorous species from Lake George and Lake Edward. *H. elegans* is a so-called generalized *Haplochromis*, a near representative of the ancestral, riverine *Haplochromis*. In our opinion the anatomical description of such a generalized species should be the basis of our studies on the comparative functional morphology of *Haplochromis*. Various arguments underlie the decision to start the description of the muscle-skeleton-ligament system with the shape of isolated skeletal elements. The methodological principles involved are deferred to the section on methods (see pp. 168–171). They essentially rely on DULLEMEIJER's holistic concepts of functional morphology (DULLEMEIJER, 1974). Here

it may be sufficient to summarize the practical arguments to describe the skeletal shape first:

1. The shape of the skeletal elements is stable with regard to the other elements in the muscle-skeleton-ligament system. At the macroscopical level a description of the system is impossible in practice without reference to the shape of the skeletal elements.
2. In literature information about morphological differences in *Haplochromis* related to functional morphology, concerns the shape of the skeletal elements.
3. In tracing functional morphological differences, skeletal elements are easier to deal with than ligaments and muscles. Figuratively speaking, differences in skeletal parts often hint at concomitant differences in the related soft tissues. Examples of trophically correlated differences in the shape of the skeleton are presented in the last section of this paper.

To read a morphological description *per se* is a rather boring affair. The usefulness of the text should be the possibility of a quick check on the definitions of the features indicated in the figures. Therefore the description-section in this paper is arranged as an encyclopedic enumeration of shape-features rather than as a continuous story. To anatomical practice the figures probably will be the most important part of the paper. With this consideration in mind much attention has been paid to the figures.

NATURAL HISTORY AND TAXONOMY OF H. ELEGANS

Among the many *Haplochromis* species living in African lakes, *H. elegans* belongs to a group of comparatively small, insectivorous species. Representatives of this trophic group are referred to as "generalized" and looked upon as the nearest lacustrine relative of the ancestral and riverine *Haplochromis* which originally colonized the incipient lakes (FRYER & ILES, 1973; GREENWOOD, 1974). The notion "generalized" and its phylogenetic implications are mainly based on similarities in cranial morphology between members of this lacustrine group and extant fluviatile *Haplochromis*, and on the assumption that these extant riverine species *(e.g. H. bloyeti)* are virtually the same as those which colonized the lakes. For a more detailed and factual discussion the reader is referred to GREENWOOD, 1974.

H. elegans (Figs 1 & 2) was first described by TREWAVAS (1933) but the species has recently been redefined in GREENWOOD's paper on the taxonomy, affinities and ecology of Lake George *Haplochromis* (GREENWOOD, 1973). Diagnostic characters for identifying adult, wild specimens are the number of teeth in the outer row of the premaxillae and

the occurrence of a small flange on the major cusp of a number of outer teeth (see section on teeth, pp. 227–231). As holds for most *Haplochromis* species, live coloration is a relative easy key to the identification, of adult male *H. elegans*. These colours are described in GREENWOOD, 1973.

In the lake *H. elegans* of 72.5 mm standard-length was the longest specimen measured (GREENWOOD, 1973) but, in tanks, they may grow much larger (*cf.* Figs 1A, B). In captivity, specimens from a

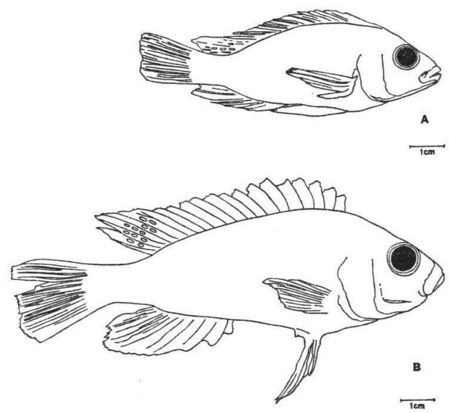

Fig. 1. Outline of *H. elegans*. Lateral view. A: wild adult specimen. B: so-called "overgrown" specimen, bred in tanks.

population caught in Lake George, and their descendants, reached standard-lengths of 108 mm. Correlated with an increase in length, a number of morphological changes occur. They include the transition of teeth, in the outer series of both jaws, from characteristic bicuspid to unicuspid. With the classical observations on morphological changes in tank-bred *Astatoreochromis* as a precedent (GREENWOOD, 1965), one should be prepared for anatomical alterations which might arise in laboratory bred generations due to a variety of factors generally cloaked in the notion "domestication". These domestication-alterations (including the "overgrown" size, as defined above) might affect morphological features characteristic for the taxonomical definition and functional morphology of "wild animals".

Geographically *H. elegans* is restricted to the Lakes Edward and George, including the Kazinga Channel connecting both Lakes (GREENWOOD, 1973). Two important papers deal with the ecology of the species in Lake George (DUNN, 1972; GWAHABA, 1973). *H. elegans* is an "inshore-species", possibly not extending further than

hundred metres from the coastline (GWAHABA, 1973). Adults preferentially feed on chironomid larvae, but other items such as dipteran emergents were regularly found as stomach-contents (DUNN, 1972; GREENWOOD, 1973).

As all *Haplochromis* species for which information is available, *H. elegans* is a female mouth-brooder (GREENWOOD, 1973 and pers. obs.). The following information on its breeding biology and growth rate is restricted to observations of animals kept in captivity. We would not unduly stress the general validity of these observations, for it is well known that a number of ecological factors influence breeding and growth data ,*e.g.* stunting, temperature, food. (For a summary see FRYER & ILES, 1973). None of these factors was standardized during our cursory observations. Courtship is essentially the same as described for other *Haplochromis* (BERKHOUDT, pers. comm.). The animals start breeding at a length of about 45 mm standard-length. A similar figure was observed for *H. angustifrons* and *H. nigripinnis* in Lake George (GWAHABA, 1973). The number of eggs vary from 11 to 59 (VAN STRATEN-WESSELING, pers. comm.). Breeding period is about fourteen days (pers. obs.) .Modal breeding frequency seems to be one nest every six weeks (VAN STRATEN-WESSELING, pers. comm.). During the first five months of their postbuccal life, *H. elegans* grows from 9 mm to about 60 mm standard-length. A mean growth of 10 mm a month accords well with the growth ratios summarized for other cichlids in FRYER & ILES (1973).

METHODS

Functional morphology means the study of the relations between forms and functions. An extensive analysis of the various methodological principles underlying morphology is given by DULLEMEIJER (1974). The methods applied in the present study are based mainly on his holistic approach to functional morphology. Following the holistic principle, the whole animal during its whole life is the final form which is to be explained in relation to all the functions which the animal has to perform. It goes without saying that such an approach in its entirety is impracticable and that certain periods from the life-cycle as well as a limited number of forms and functions are to be selected. The point in this theoretical consideration is to realize that the periods, functions and forms which are *excluded* do bear relations to the forms studied. Accepting this holistic idea involves two important logic consequences. First, only a partial explanation of the selected forms is to be expected from the selected functions. Second, no final explanation will be found in proceeding analysis. In holistic functional morphology analysis is

merely used as a technical necessity and practical restriction, not as a method in the hope to discover the explanation at a certain level of analysis.

As this paper deals only with the shape of skeletal elements, a discussion on the concept "form" would seem sufficient, leaving the notions "function" and "relation" aside for the moment. The selection of forms is, however, greatly determined by the selected functions and the presupposed kind of relations between these forms and functions. The functional morphological studies on *Haplochromis* will be restricted to the muscle-skeleton-ligament system of the head as the form to be explained in terms of mechanical relations to functions such as feeding and respiration. It is obvious that these selections of forms, functions and relations are mutually dependent, although the coherency is, as yet, mainly intuitive. The ultimate aim of the study on *Haplochromis* is to formulate this coherency, but at this incipient phase analysis of forms and functions are the first steps to be made. The present paper represents the first part of a description of the form, *viz.* the muscle-skeleton-ligament system in the head of *adult Haplochromis elegans*. This form will be divided into units which are determined on the basis of their mechanical properties. The units discerned at the first step of form-analysis are called *primary elements*. Three classes of primary elements, each with its own mechanical properties, are discerned: muscles, connective tissue elements and skeletal elements. The mechanical definition of muscles and connective tissue is, as yet, not relevant. Inside the muscle-skeleton-ligament system, primary skeletal elements represent those mechanical units of which the shape is considered to be unchangeable for the period of observation and within the limits of observational techniques. Primary elements may, at a second step, again be divided into spatially separated units called *secondary elements*. All elements, primary as well as secondary, possess at least three form-features: shape, structure and position. Shape describes the external limits of the element; structure is a description of the content, position locates the element inside the form to which it belongs. For primary elements this form is the muscle-skeleton-ligament system. For secondary elements it is the primary element. A complete morphological description of an element involves all three features. This paper describes the shape of the primary skeletal elements in the head of adult *Haplochromis elegans*. The primary elements are grouped in so-called apparatuses. An apparatus is a composition of elements serving a part-function inside the system. Whereas primary elements are the first level units in *analysis*, an apparatus may be conceived as the first level units in the *synthesis* from primary elements to the system. The apparatuses as defined in this paper are not complete. Only

those apparatuses are mentioned which coincide with a practical subdivision of the system during dissection and only the skeletal elements of the apparatuses are included.

Providing a description of the skeletal primary elements, instrumental in screening functional relevant differences between *Haplochromis* species, was a task beset with two main difficulties. First: the skeletons of *Haplochromis* species greatly resemble each other at first glance. Second: the terminology on fish-anatomy is rooted in formal comparative anatomy. As both morphologies persue different aims, it is not probable that form-elements distinguished in *comparative* morphology coincide with those suitable for *functional* morphology. One example may amplify this statement. When dealing with comparative morphology the shape of the neurocranium is described on the basis of its constituent "bones" such as parasphenoid, epiotic, vomer. In describing the neurocranial shape with a functional interpretation as aim, the shape and position of surface-projections, deepenings and articulation facets are relevant. These surface-sculptures are related to the mechanical functions of the neurocranium or the connected elements: *e.g.* ridges serve muscle-insertion, facets determine movement-possibilities of attached elements. In our approach vomer and parasphenoid may represent secondary elements of the neurocranium. Their *functional* significance may be later entered upon when dealing with the relation between function and *structure* of the primary elements.

Morphological differences between *Haplochromis* species are small and often quantitative only, whereas intraspecific variability appears to be large (see morphometrical data on taxonomic characters in the various papers of GREENWOOD on the revisions of the Lake Victoria and the Lake George *Haplochromis* species and monotypic genera). Excepting the jaw-teeth and trends in the gross anatomy of the neurocranium, jaws and the lower pharyngeal element (GREENWOOD, 1974), little is known about morphological differences which accrue from functional morphology of haplochromine cichlids.* From cursory observations, however, it is clear that such differences do exist. They are small and quantitative, and often deal with very restricted parts of the surface sculpture. These observations forced us to describe shape extensively.

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* LIEM (1973) contains some information on the anatomy and functions of *H. burtoni* and other cichlids. Concerning cichlids other than haplochromine species, GOEDEL's papers on *Tilapia* species are the nearest to our subject (GOEDEL, 1974a, b). As far as we know these papers contain the only extensive description of the muscle-ligament-skeleton-nerve system in the head of a cichlid fish. For a review on literature about the anatomy of the head of a cichlid fish the reader is referred to GOEDEL, *op. cit.*

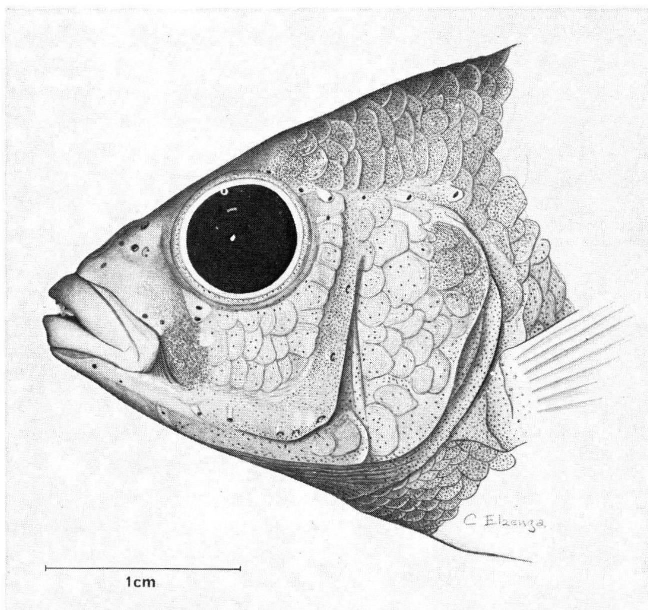


Fig. 2. Head of an adult, wild *H. elegans*. Lateral view.

The efficiency of comparative investigations greatly relies on the discriminating power of the nomenclatorial tools. The problem remains how deep the initial description should go and on what species it should be based. Concerning the species, the choice for *Haplochromis elegans* is based on two arguments. First this species represents a generalized *Haplochromis* in the evolution-studies of GREENWOOD (see p. 166). Second, sufficient material both alive and fixed was available. Live material allows us to investigate the activity as well which remains an essential condition in the analysis of function. Except for the teeth, we have not tried to give an osteological definition of the species. Neither could it, as yet, be the aim of the present paper to provide a full description of the insectivorous tropihc type of *Haplochromis*. With an intuitive idea in mind as to which parts of the surface sculpture could be functionally relevant, these parts were topologically defined and figured for *Haplochromis elegans*. The description of these parts is restricted to those features instrumental in the topological recognition of the part. In applying the description to a limited number of trophically different *Haplochromis* species, it was checked whether the topological definitions based on *Haplochromis elegans* were sufficient to trace similar sculptural features in other species. As has been stated before, during these comparisons trophically relevant differences were observed. Two examples are given on pp. 244–260.

NOMENCLATURE: DEFINITION OF TOPOGRAPHICAL AND MORPHOLOGICAL TERMS

Editorial Notes

Concerning the text:

1) *Morphological terms in italics.* Throughout the text a term denominating a shape-feature is printed in italics on the place where this feature is defined and described.
2) *Reference to figures.* Each section has its own figures. Reference to these figures is given in the section-heading. Reference to shape-features demonstrated better in other figures, is found in the text near the main treatment of this feature.

Concerning the figures:

1) *Elevated "d" in abbreviations.* An elevated "d" at the end of an abbreviation refers to the directional form of the term. E.g.: susp. = suspensorial, susp.^{d} = suspensoriad. The difference between positional and directional terms is explained on pp. 172–173.
2) *Fitting.* Many figures are based on stereoscan-photographs which can only be made from macerated skeletal preparations. In such preparations hardly any cartilage is left. The open space into which the cartilage fitted originally, is indicated as "fitting".

3) *Source of the figures.* Data on the source of the figures are given in a separate table at the end of this paper. These data concern the kind of preparation from which the figure was drawn; the number and the standard-length of the specimen from which the preparation was obtained.

Directions, positions and sections (Fig. 3A & G)

As has been explained in the preceding chapter, each element at every moment has three aspects: position, shape and structure. The position of an element is either described as absolute or as relative. The *absolute position* is defined as the one with regard to the neurocranium, the relative position locates an element to another element, except the neurocranium. On each element a reference-grid is defined. The one on the neurocranium is called the *absolute reference-grid*, that on another element is a *relative reference-grid* and is called after the element. The relative reference-grid is derived from the absolute position of conspicuous sculptures of the element in a non-expanded head. The relative grid is further defined in such a way, that topological description of the surface-sculpture remains as simple as possible, *e.g.* by making reference planes coincide with the planes of easiest observation of the isolated element. In studying shape and structure of an element, it is nearly always removed from its position inside the whole. In the present paper these aspects are therefore described with regard to the element's relative reference-grid. *E.g.*: the posttemporal is a Y-shaped element (Fig. 43). The plane through the arms of the Y faces, with regard to the absolute reference-grid, rostrad-laterad. The easiest way of observing the element is in a view perpendicular to this plane through the arms. In our opinion the description of the element's shape is much easier to follow when this plane of observation is defined as the posttemporal's relative transverse plane instead of using the absolute reference-grid.

Another reason for using an element-bound relative reference-grid for describing its shape and structure is, that the directions and positions of the features discerned in shape and structure would change with every change in position of the element, if they were defined with regard to the neurocranium.

In the terminology used, direction is distinguished from position by using different suffices. The classical terms later*al*, dors*al* *etc.* refer to position; later*ad*, medi*ad* *etc.* to directions. A is *external* with regard to B, when A is nearer to the border of the element. Border refers to the outline as seen in the view under discussion. *Internal*, *externad* and *internad* are defined similarly .Double terms like medio-ventrad and ventro-mediad are not synonymous (Fig. 3A). Rostro-ventrad refers to a direction in which the ventrad component is the dominant one, con-

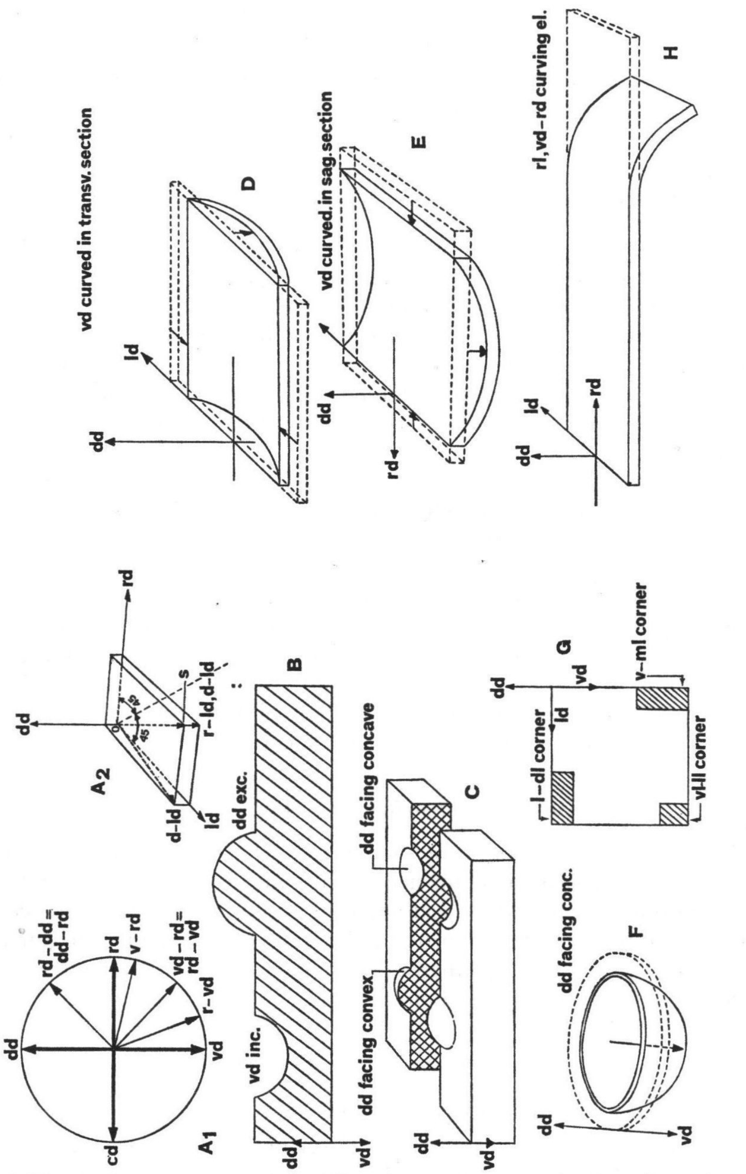


Fig. 3. Nomenclature on topography, directions and shapes. A_1: two dimensional directions; A_2: three-dimensional direction. The direction of OS is given as: rostro-laterad, dorso-laterad. B: excurvation and incurvation. C: concave and convex. D, E: two possibilities of simple curvature of an element as a whole. F: spherical curvature of a whole element. G: occupation of corners. H: curvature of terminal parts. *E.g.* Rostrally the element curves ventrad-rostrad.

versely ventro-rostrad means the main direction to be rostrad. When neither of the directions is dominant, it will be described as ventrad-rostrad (= rostrad-ventrad). A direction or position with (vectorial) components in two planes of the reference-grid, will be described on the basis of the directions or positions of each of the components (Fig. 3A: OS directs rostro-laterad, dorso-laterad). The external part of an element is referred to as ventro-medial when it includes the ventral-medial corner and when the ventral-dorsad length exceeds the medial-laterad length (Fig. 3G). When neither of the lengths dominates the section is located as being medial-ventral.

The *longitudinal axis* runs approximatively in the length and through the core of an element. *Cross-sections* are sections perpendicularly to the longitudinal axis. Other sections are named after the relative or absolute reference plane with which they coincide or after the facing vector of the section's plane with regard to the relative or absolute reference grid.

A morphological feature of an element may be called after that element or after another element to which it bears a relation; *e.g.* "the neurocranial apophysis" could either be a process on the neurocranium or a process on another element directing towards the neurocranium. In the present paper this confusion will be avoided by applying different suffices for direction and position, following the idea which has been exposed above for the general terminology on position and direction (caudal-caudad, *etc.*). *E.g.*: the articulation surface of the interhyal with the suspensorium is to be referred to as the interhy*al* suspensori*ad* articulation facet.

Topographical sections (*e.g.* Figs 13 & 14)

The series: *region*, *area*, *sector*, form a descending hierarchial order. The more extensive elements are divided into regions; regions may be split into areas, areas into sectors. Whereas regions, areas and sectors have boundaries defined through clear-cut morphological features, a *zone* merges into an adjoining one without a morphologically traceable shape interposed between them.

Shapes and their directions

Directions of planes, openings and flattened shapes

The directions of a plane may be described either by the direction of a vector in the plane or the direction of a vector perpendicular to the plane. The former one is called the *direction of the plane*, the latter one the *facing vector of the plane*. In the same way openings are charac-

terized by the direction or facing vector of a plane covering the opening.

The direction of a flattened shape is described by the facing vectors of the planes between which the shape seems to be compressed.

Curved shapes and their directions (Fig. 3B–F, H)

Nomenclature describing curvature comprises: concave (concavity), incurved (incurvation), convex (convexity), excurved (excurvation) and curved. Concave and convex are applied to three-dimensional curvatures. Incurved and excurved refer to two-dimensional ones. The directions of concave and convex surfaces are described as the direction of the facing vector of the plane covering the margins of the curvature away from the centre of the element (Fig. 3C). Excurvations and incurvations are described as the direction in which the curvature deviates from the main outline under discussion (Fig. 3B). Elements as a whole may be curved. Two-dimensional curvature of whole elements is discussed on the basis of the outline of a cross section perpendicular to the direction for which the element is straight. The two-dimensional curvature is then described as the direction of curvation of the cross-sectional outline from a theoretical flat state to the actual one, leaving the margins of the elements in the original plane or on the original line (Fig. 3D, E). Flattened elements may be saucer or bowl-shaped. Such curvature is described with the facing vector of the concave side (Fig. 3F).

Finally a terminal part of an element may demonstrate flexure away from the main rectilinear direction. This is described by saying that the element for this terminal part curves to the final direction of the deviating part (Fig. 3H).

MATERIAL AND TECHNIQUES

All specimens of *H. elegans* used for this study were caught in Lake George (Uganda). Animals were obtained from the British Museum (Natural History), or have been collected by Barel in 1972 during a visit to Lake George as guest of the hydrobiological team which, at the time, was investigating the lake as part of the International Biological Programm. Beside a collection of preserved *H. elegans*, a small stock of live animals was successfully forwarded to our institute.

As far as possible the preparations of skeletal elements on which this study is based, will be preserved in the condition in which they were studied and figured. For all preparations it has been registered to which specimen they belonged. From the original intact specimen x-ray as well as black and white exposures from different directions

were made. Generation, and taxonomical measurements as defined by GREENWOOD, 1973: 145, are recorded. In this way it will be possible at any future date to obtain further information, either on the preparation itself or on the specimen to which it belonged. This may become necessary because:

1. Differences between *Haplochromis* species are small and misidentification could be involved, especially between *H. elegans* and *H. aeneocolor* or *H. macrops*.
2. The preparation may belong to a class for which no further specimens are available, *e.g.* overgrown specimens of the first generation of laboratory-kept *H. elegans*.
3. One of the eventual goals of the current investigations is to pinpoint functionally relevant differences between trophically different *Haplochromis* species by means of a comparative method. Therefore, it must remain possible to rule out differences related to domestication, ontogeny (including overgrown size) and intraspecific variability.

Four kinds of preparation-techniques have been used to study the shape of the skeletal elements:

1. Serial-sectioning whole heads embedded in plastic, following the technique described by ANKER, (1974).
2. Bone-cartilage in toto staining. Whole mounts in which the skeleton was differentially stained for bone and cartilage with alizarine and alcian blue respectively, were obtained following SIMONS & VAN HORN (1971).
3. Maceration.
4. Gold-coated preparation and stereoscan photographs. An important part of the skeletal preparations obtained by maceration, has been coated with gold using an Edwards vacuum coating unit, model E12E (London) and E500 Diode sputtering system, A. de Jong T.H.B.V. (Rotterdam). Before coating, the elements were carefully defatted, *viz.* by keeping the preparations overnight in ehter. From the coated elements low power stereoscan-photographs were taken, using a "Cambridge stereoscan" scanning electron microscope. A good overall picture of the elements was obtained for each side by composing series of stereoscan-photographs overlapping each other for about 20%, mostly at a magnification of 50 × or 20 ×, depending on the size of the element. Elemenets exceeding a horizontal radius of 10 mm and/or a depth of 8 mm were fractionized. A number of separate details, such as teeth and articulation surfaces, was studied from collages of photographs made at higher magnifications.

Studying the shape of skeletal elements, gold coated preparations and their stereoscan-photographs yielded far more telling information

than the other techniques. In alizarine, alcian blue preparations surface-shape is difficult to discern from translucent underlying structures. In macerated preparations. however, cartilage is often damaged or completely lost. For this reason alcian blue, alizarine preparations are necessarily experimented to obtain a complete picture of the shape of elements. In dry uncoated skeletal elements the opacity of surface ornamentation obliterates their real shape. Reconstruction of surface shape from serial section is very time-consuming and will never reveal as much details as stereoscan-photographs. The main use of the serial sections was to provide cross-sections of skeletal elements, facilitating a three-dimensional interpretation of the figures and to obtain additional information in the determination of articulation-surfaces. It goes without saying that stereoscan-photographs are much more easily discussed, compared and copied than the original preparations which are often small and vulnerable. By far the greatest part of the figures is based on stereoscan-photographs combined with microscopical observation on the preparation from which the photograph was made (*cf.* table of preparations, pp. 263–265).

SHAPE OF THE SKELETAL ELEMENTS

Topography of the primary elements and definitions of the apparatuses

The absolute reference-grid

The reference planes through the neurocranium are, by definition, the absolute ones for positions and movements in the fish-head. The neurocranial features through which these planes are defined, are discussed in the section on the neurocranial shape. The *sagittal plane* is taken as the neurocranial plane of symmetry. Perpendicular to this plane and through the dorsal border of the parasphenoid ventral crest (p. 183) runs the *horizontal plane.* The *transverse planes* are defined perpendicularly to both horizontal and sagittal plane.

Topography of the primary elements and definitions of the apparatuses (Fig. 4)

The topography of the primary elements, as discussed in this section, refers to an approximate indication of their absolute positions in a so-called "non-expanded head". The elements are left in such a position after quiet anaesthesia. A precise quantitative definition of positions can be given only after describing the shape of the elements.

From the lateral margin of the neurocranium the plate-shaped *suspensorium* extends latero-ventrad. Rostral and caudal to the eye, the suspensorium articulates with the neurocranium. Movably attached to the caudal margin of the suspensorium is the *gill-cover,* a

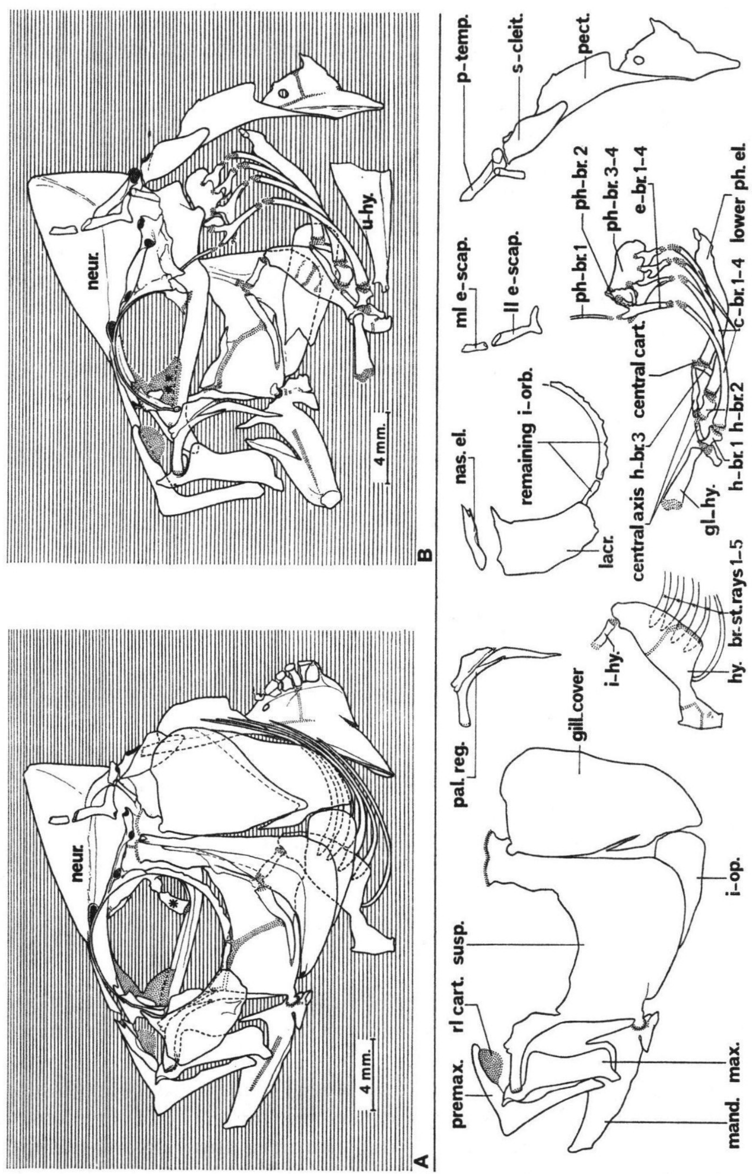


Fig. 4. Primary skeletal elements in situ. A: non-expanded head. Absolute lateral view. * marks the basisphenoid peduncle. The hyoid-branchiostegal apparatus has been drawn after another specimen. B: expanded head. Absolute lateral view. From the left side of the head the following elements have been removed: suspensorial apparatus (except for the palatine region), nfraorbital apparatus, nasal, hyoid-branchiostegal apparatuses, mandible. From the right side have been removed: maxilla, branchiostegal rays, girl-cover, branchial apparatus (except for the central series) and shoulder-girdle apparatus. ** marks the interorbital cartilage.

flat caudad continuation of the suspensorium. The *interoperculum* is a flat oblong element, partly medially partly extending medio-ventrad to the ventral margin of the suspensorium. Gill-cover and interoperculum together with the suspensorium constitute the skeletal elements of the *suspensorial apparatus*.

The *lower jaw* is made up from left and right *mandible*, together forming a rostrad curved arch. The mandibles articulate with the rostral-ventral corners of the suspensorium and bear teeth dorsally. The *upper jaw* is built up from the unpaired *rostral cartilage* and left plus right *premaxilla* which together make a dorso-rostrad curved arch, ventrally provided with teeth. The rostral cartilage is situated at the distal ends of the caudad-dorsad directed spines of the premaxillae. The upper jaw articulates with the rostral-dorsal face of the neurocranium by means of the rostral cartilage. Dorsally and more or less parallel to the laterally visible part of the premaxilla, the *maxilla* is found which articulates rostral-laterally with a rostral process of the suspensorium and rostral-medially with the premaxilla. Maxilla and premaxilla constitute the skeletal elements of the *maxillary apparatus*. The *jaw apparatus* contains the skeletal elements of the maxillary apparatus and the mandible.

The *hyoid arch* lies caudal to the lower jaw in the floor of the mouth in a parahorizontal plane. The arch consists of four primary elements: left and right hyoid plus left and right interhyal. Both *hyoids* are rostrally symphyseally connected and diverge caudad to meet the medial side of the suspensorium. The hyoid articulates with the suspensorium by means of the small rod-shaped *interhyal*. For its skeletal parts the *hyoid apparatus* (Fig. 5) is composed of hyoid and interhyal.

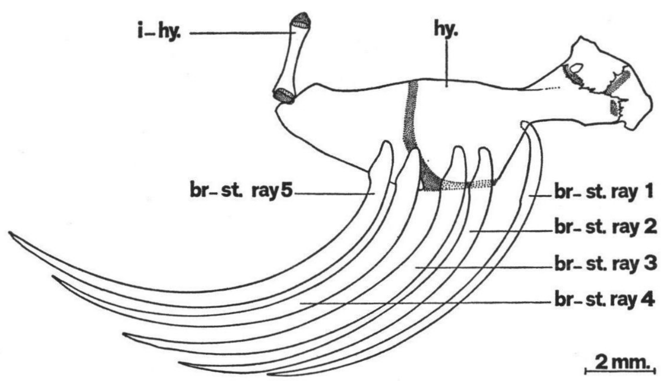


Fig. 5. Right hyoid and branchiostegal apparatuses. Absolute lateral **view.**

The hyoid bears a series of five slender spinous *branchiostegal rays*. Hyoid and rays form the skeletal elements of the *branchiostegal apparatus* (Fig. 5). Caudally in the buccal cavity the *branchial basket* is found. It is formed by 4 gill-arches on each side and ventrally a series of unpaired, sagitally situated primary elements (the *central series*). The *branchial apparatus* (Figs 6 & 7) contains the skeletal elements of the four gill-arches from one side and the elements of the central series. As compared to other apparatuses defined in this section, the branchial apparatus contains by far the largest number of primary elements: 18. Each *gill-arch* can be described as a chevron of articulating elements. The gill-arches are situated in rostro-laterad facing, parallel planes. Excepting the fourth arch which has no hypobranchial, each arch is formed by four units: *hypobranchial*, *ceratobranchial*, *epibranchial* and *pharyngobranchial* (Fig. 4). As the pharyngobranchials of the third and fourth arch are fused (Fig. 6), they constitute, according to our

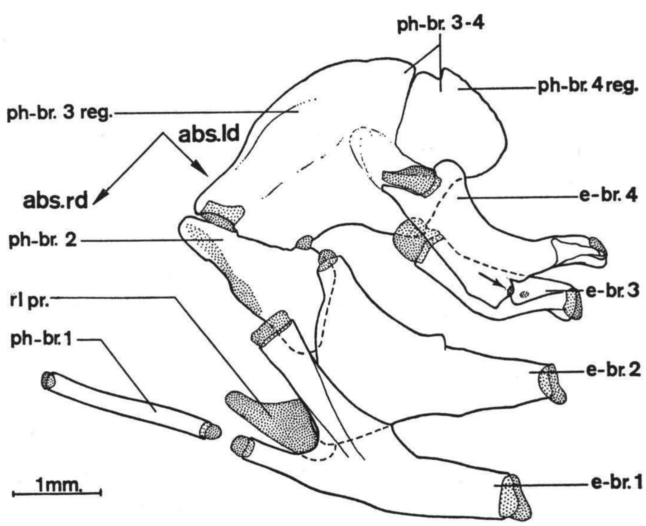


Fig. 6. Dorsal half of the left branchial apparatus. Absolute dorsal view. The arrow in epibranchial 4 indicates the epibranchiad 3 articulation facet.

method, one primary element which will be referred to as *pharyngobranchial 3,4*. Pharyngobranchial 3,4 and pharyngobranchial 2 bear teeth on their ventral faces. GOEDEL (1974b) refers collectively to pharyngobranchials 2,3,4 as ossa pharyngia superiores. Pharyngobranchials 1 and 3,4 connect the branchial basket with the skull. The

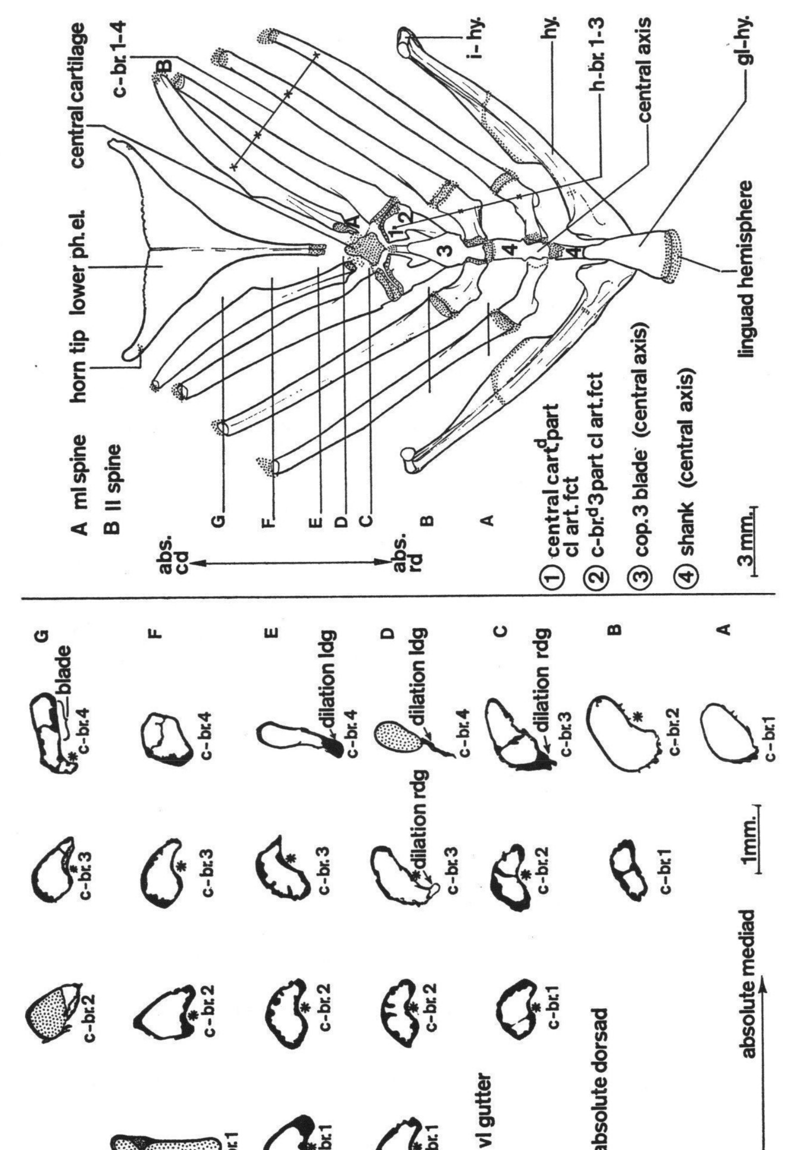


Fig. 7. Right: ventral half of the branchial basket and hyoid arch. Absolute dorsal view. Left: absolute transverse sections through the ceratobranchials. The sections are not derived from the preparation drawn on the right side of the figure but from serial sections of a complete head in a non-expanded situation.

hypobranchials and ceratobranchial 4 form articulations of the gill-arches with elements from the central series. In a rostral-caudad order the primary elements of the central series are: *glossohyal*, *central axis*, *central cartilage* and *lower pharyngeal element* (os pharyngius inferius, GOEDEL 1974b) (Fig. 7). The last one is a conspicuous element with an extensive dorsad, triangular, teeth-bearing face. The *urohyal* is a flat sagittally situated triangular element, ventral to the branchial basket (Fig. 4B).

The skeletal elements of the *shoulder girdle apparatus* consist of three primary elements. Left and right shoulder girdle apparatuses together form a more or less transverse arch *(shoulder girdle)* which, by definition, limits the head caudally. Dorsally in the shoulder girdle apparatus the Y-shaped *posttemporal* connects the shoulder girdle apparatus with the neurocranium. By far the largest part is the ventrally situated *pectoral element*. Pectoral and posttemporal are connected through the *supracleithrum*.

In a number of primary elements the lateral line canal dominates. These elements are collectively referred to as: the primary *lateral line elements*. Lateral to the spine of the premaxilla the *nasal element* is found. Except for a dorsal zone, the *infraorbital apparatus* (Fig. 8) forms a series of primary lateral line elements around the eye. The extensive rostral infraorbital is called *lacrimal*. Two *extrascapulae* lie in the skin dorso-medially to the lateral part of the posttemporal.

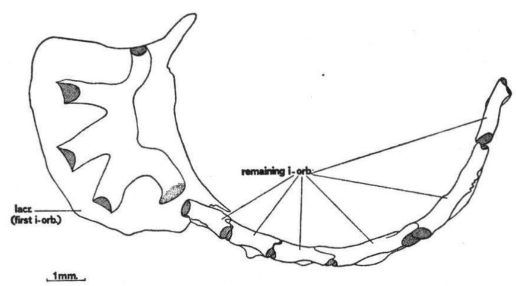


Fig. 8. Left infraorbital apparatus. Absolute lateral view.

A *pharyngeal tooth* is a term for a tooth on the pharyngobranchials 2 & 3,4 and on the lower pharyngeal element. A *jaw-tooth* is a tooth from the premaxilla or from the mandible.

Neurocranium (Plates I & II; Figs 9–12)

Outline and orientation (Pls. I & II). The general shape of the neuro-

cranium approximates to a rostrad pointing symmetrically bisected cone whose plane of bisection faces nearly ventrad. The plane of symmetry of the neurocranium is the absolute sagittal plane.

In a lateral view a large fenestra is observed. This *interorbital fenestra* perforates the sagittal plane and connects left and right orbita. The fenestra is limited ventrally by the sagittal, horizontally running *parasphenoid bar*. Two more conspicuous features are, for orientation purposes, marked in the lateral view: 1. a striking dorsad curved semicircle forming the lateral edge of the *orbital margin* (margo supraorbitalis ossis frontalis, GOEDEL 1974a); 2. a dorsad protruding sagittal crest on the caudal half of the skull: the *supraoccipital crest.*

The neurocranial regions (Plate I). For descriptional convenience the neurocranium is divided into four regions. Between the transverse planes through the rostral and caudal ends of the orbital margin, the *orbital region*; rostral to the orbital region the *ethmoidal region*; caudad the *otical* and occipital regions successively. The *occipital region* is the caudal face of the neurocranium.

Orbital region (Fig. 9). The orbital margin terminates rostrally in the *preorbital process*, caudally in the *postorbital process*. The orbital margin lodges three of the six paired *neurocranial lateral line foramina (NLF)* on its dorsal face (Pl. IA). On the rostral-dorsal section of the margin the mainly rostrad opening NLF_1 (Fig. 12) is found, followed caudally by NLF_2 of which the opening faces latero-rostrad. NLF_3 opens mainly laterad and close to the edge of the caudal-dorsal section of the orbital margin. The *nasad process* (Fig. 12) is found as a rostrad protuberance on the rostral half of the orbital margin halfway between NLF_1 and the preorbital process. From the caudal half of the orbital margin, two mainly caudad running crests originate (Pl. IA): 1. the horizontal *parietal crest* of which NLF_3 marks the rostral origin; 2. halfway along the caudal half of the orbital margin the *lateral line crest* begins.

Ventrally as well as dorsally the parasphenoid bar bears a sagittal crest. The *parasphenoid ventral crest* (Pl. IC) starts rostrally in the orbital region as a shallow process; caudad it gradually deepens. The line marking the transition from the ventral crest to the body of the parasphenoid bar constitutes, by definition, the absolute *rostrad-caudad directions* in the fish-head. All through the orbita the parasphenoid bar bears the *parasphenoid dorsal crest* (Pl. IC). Caudally on the dorsal crest the flat, sagittal *basisphenoid peduncle* (GOEDEL, 1947a) (Fig. 4A, marked with an *) originates and runs caudo-dorsad to the left and right, latero-dorsad directed *basisphenoid wing*. The wings separate the rostral part of the cavum cranii from the *caudal myodome*. The peduncle

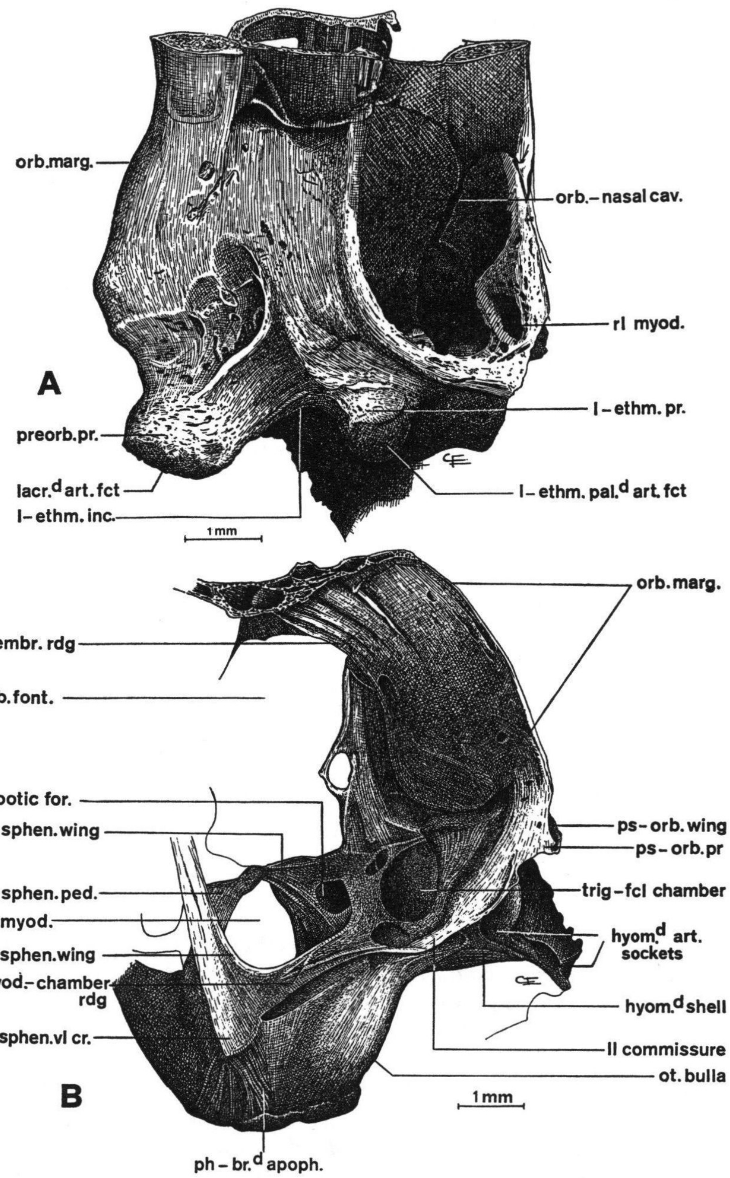


Fig. 9. A: rostral wall of the neurocranial left orbita. Ventral-caudal view .B: caudal half and mainly left parts of the neurocranium. Ventro-rostral, latero-rostral view. The figure demonstrates shape-features in and around the caudal orbital wall.

is the rostral part of the wall between left and right caudal myodome. Somewhat rostral to the origin of the peduncle a laterad enlargement of the parasphenoid bar (the *parasphenoid wing*, Figs 9B & 10) starts as a crest of little transverse depth. Caudally the wing extends rather abruptly broadly laterad-dorsad and forms the oblique floor of the myodome. In the lateral-ventral corner of the entrance to the myodome. The rostral margin of the parasphenoid wing splits off a dorsad-laterad curving ridge (the *myodome-chamber ridge*) which forms the lateral border of the myodome-entrance. Between the dorsal end of this ridge and the basisphenoid wing the large *prootic foramen* opens mainly ventrad. The rostral margin of the parasphenoid wing proceeds laterad as the mainly horizontal *lateral commissure* (GOEDEL, 1974a following BERTMAR, 1959) (Figs 9B & 10) which forms the rostral boundary of a large foramen, opening caudo-ventrad into the otic area (the *chamber-floor foramen*, Fig. 10). The *trigemino-facial chamber* is a cave-like caudad interruption of the caudal orbital wall, dorsal to the lateral commissure. The medial wall of the chamber is perforated by a number of foramina. Medially the caudal wall of the orbita is interrupted by the unpaired huge entrance to the cavum cranii: the *orbital fontanelle* (ALLIS, 1903). Besides the orbital fontanelle and the trigemino-facial chamber a number of small foramina and impressions of nerves are found in the caudal orbital wall. These are not described in the present paper.

From the dorsal-lateral corner of the orbital fontanelle a ridge runs rostrad in the medial part of the ceiling of the orbita: the *membrane ridge* (Fig. 9B). The left and right ridges converge rostrad and at their meeting point the caudal-dorsal end of the *interorbital cartilage* (Fig. 4B) is found. The interorbital cartilage is a plate separating the rostral parts of the left and right orbita sagitally.

The *orbito-nasal cavity* (DAGET, 1964) is a rostrad tapering fossa in the medial part of the rostral orbital wall. The cavity is perforated rostrally by the *foramen olfactorium advehens* (DAGET, 1964) (Fig. 12A) which opens into the ethmoidal region. A small semiconical calyx opens caudad on the medial wall of the orbito-nasal cavity: the *rostral myodome*. On the ventral margin of the rostral orbital wall two processes, each provided with a ventrad facing articulation facet, are found. The latero-ventral corner forms the preorbital process (p. 183) which bears the *lacrimad articulation facet*. Ventrad and near the lateral-ventral corner of the orbito-nasal cavity there protrudes the *latero-ethmoidal process* which bears the *lateroethmoidal palatinad articulation facet*. Between the latero-ethmoidal process and the preorbital process the margin is strongly incurved dorsad: the *lateroethmoidal incurvation*.

Otic region (Figs 10 & 11). The series of mainly rostrad-caudad

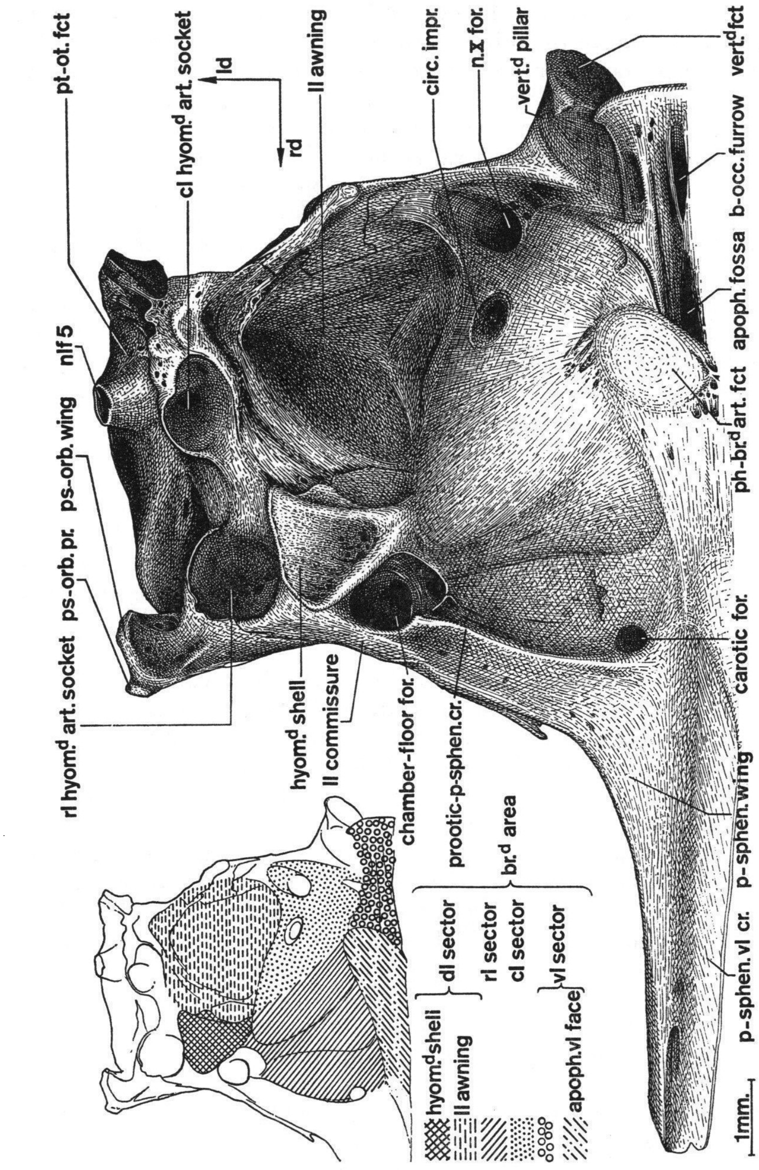


Fig. 10. Left half of the otical region of the neurocranium. Mainly ventral view.

running crests (supraoccipital, parietal and lateral line crest) divide the external surface of the otic region into four areas (Pl. IC): The *supratemporal area* (= fossa supratemporalis, GOEDEL, 1974a; supratemporal groove, ALLIS, 1903) lies between the supraoccipital and parietal crest. The *temporal area* (= fossa temporalis, GOEDEL, 1974a; temporal groove, ALLIS, 1903; posttemporal fossa, LIEM, 1970) lies

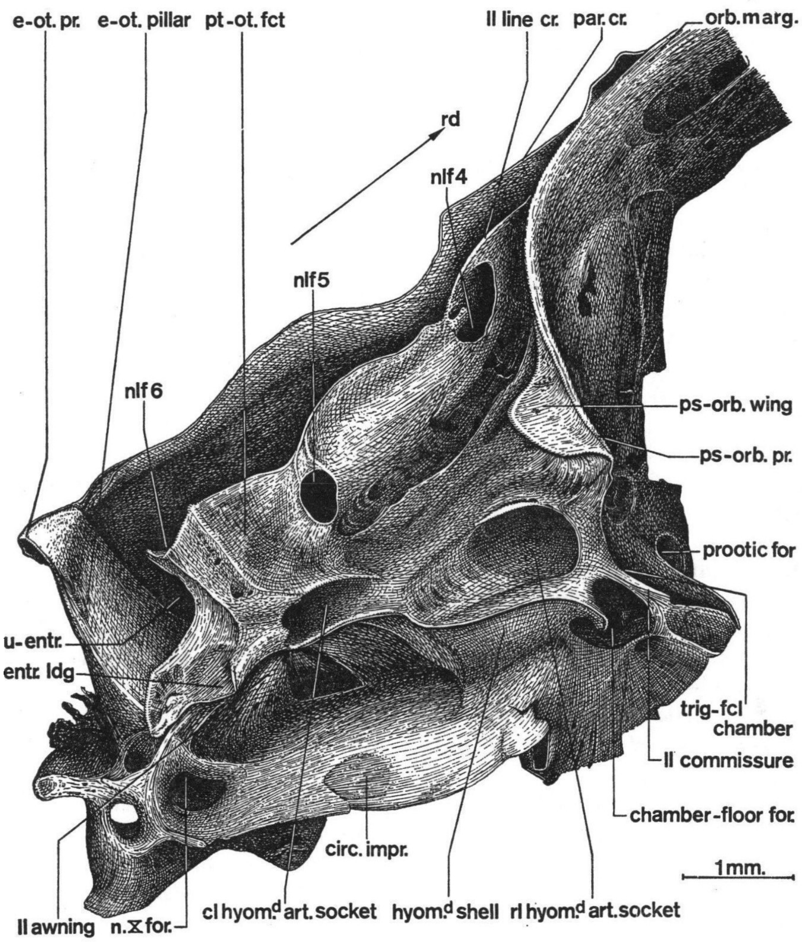


Fig. 11. Right dilatator and temporal areas of the neurocranium. Caudal-lateral, ventral-lateral view. The ventral part of the branchiad area and the medial part of the supratemporal area have been cut off.

between the parietal and lateral line crest. The *dilatator area* (dilatator groove, GOEDEL, 1974a; ALLIS, 1903) is a narrowing space between the lateral line crest and the caudal, mainly vertical part of the orbital margin. Ventrally the dilatator area is bordered by two articulation sockets (hyomandibulad articulation sockets). The *branchiad area* is the surface of the otic area ventral to the floor of the sockets and extending as far as the sagittal plane.

The caudal margin of the supratemporal area runs caudo-laterad and terminates laterally in the flattened, horizontal *epiotic process* which forms the caudal end of the parietal crest. Medial to this process this margin bears a caudad protuberance of variable size: the *epiotic protuberance* (Pl. IIB).

Two storeys can be distinguished in the floor of the temporal area: the triangular *rostral floor* being higher than the *caudal floor.* A steep wall leads from the rostral to the caudal floor. In caudal view the entrance to the temporal area is U-shaped (the *U-entrance*) (Pl. IIB). The medial arm of the U is a dorsad converging pillar (the *epiotic pillar*) which bears the epiotic process and protuberance on top. The shorter, lateral arm of the U-entrance is the caudal border of the lateral line crest. It terminates in the dorsad facing NLF_1. The horizontal part of the U bears over its greater, lateral part the caudad extending *entrance ledge* (Pl. IIB) which is best developed in the lateral-ventral corner of the U.

The *postorbital process* is formed by the caudal-ventral part of the orbital margin and is provided with the caudad directed *postorbital wing*.

The hyomandibulad articulation sockets on the ventral margin of the dilatator area are two dome-shaped cavities interconnected by a shallow and inconspicuous groove. The *rostral hyomandibulad articulation socket* is a spherical caudo-laterad facing cavity, caudal-ventral to the postorbital process. In contrast to the caudal socket, the rostral one has a well-developed ventral floor which is part of a laterad extending flare: the *hyomandibulad shell* (see also below). The *caudal hyomandibulad articulation socket* is smaller, ovoid in outline and faces latero-ventrad, rostro-ventrad.

The *lateral line crest* (Pl. IA) bears the three caudal neurocranial lateral line foramina (NLF_{4-6}). The laterad facing NLF_4 is situated near the rostral origin of the crest. The dorsad facing NLF_6 (Pl. IC) marks the dorsal-caudal corner of the crest. Between $NLF_{5|6}$ the caudal quarter of the lateral line crest is comprised. NLF_5 opens laterad (Pl. IB). The *pterotic facet* (Pl. IA) is a roughly sculptured, laterad facing surface between the caudal edge of the lateral line crest and the margin connecting NLF_6 and NLF_5. The rostral wall of the facet is the caudal

wall of NLF_5, the ventral margin of the facet is the caudal part of the ceiling of the caudal hyomandibulad articulation socket.

For descriptional convenience four sectors will be distinguished in the branchiad area (Fig. 10). The predominantly ventrad facing *dorsal sector* extends laterad to the line connecting the chamber-floor foramen and a foramen ventral to the epiotic pillar *(the nerve X foramen)*. In ventral view, two concavities, triangular in outline, are observed in the dorsal sector. The rostral and smaller one has its base situated laterally and top medially and forms the *hyomandibulad shell* (see also above). The rostral margin of the shell borders the chamber-floor foramen caudally. Far larger and deeper than the hyomandibulad shell is the second concavity (the *lateral awning*). The triangular outline of this awning is reversely orientated with regard to the shell-triangle. The base of the awning-triangle lies medially and is formed by the line between the chamber-floor foramen and the nerve X foramen. The top is at the lateral-ventral corner of the U-entrance.

The ventral face of the otic region is dominated by the massive pyramidal *pharyngobranchiad apophysis* (Pl. IA), forming one of the salient features of the cichlid neurocranium. The apophysis bears the left and right *pharyngobranchiad articulation facets* on its caudal-ventral corner. Near the dorsal-caudal end of the parasphenoid ventral crest the *carotic foramen* (foramen caroticum externum, GOEDEL, 1974) is found on the lateral face of the branchiad area. Between the carotic foramen and the chamber-floor foramen the latero-caudad protruding *prootic-parasphenoid crest* runs predominantly dorsad.

The *rostral sector* of the branchiad area is a triangle between the prootic-parasphenoid crest and the lines from the carotic foramen and from the chamber-floor foramen to the pharyngobranchiad articulation facet. The main and rostral part of the rostral sector is flat and faces ventro-laterad. However, the caudal margin between the chamber-floor foramen and the pharyngobranchiad articulation facet is bullate, excurved in horizontal section and is referred to as the *otic bulla*. The remaining lateral part of the branchiad area is the *caudal sector*. It is contained between the otic bulla, the line connecting the chamber-floor and nerve X foramina and the lateral margin of the basioccipital furrow (see below). Rostral-ventral to the nerve X foramen the caudal sector bears the *circular impression*. The part of the otic region that lies medial to the rostral and caudal sector is the *ventral sector*. Caudal in this ventral sector, the ventrad facing *basioccipital furrow* is found between the pharyngobranchiad articulation facets and the ventral margin of the caudad facing circular vertebrad concavity (see below). The furrow leads rostrad to an impression in the caudal wall of the apophysis referred to as the *apophyseal fossa*. The remaining

part of the ventral sector is a mainly ventrad facing triangle between the caudal-dorsal corner of the parasphenoid ventral crest and the lateral corner of the pharyngobranchiad articulation facet: the *apophyseal ventral face*. From its ventral origin at the parasphenoid ventral crest the apophyseal ventral face slopes gently upwards to the pharyngobranchiad articulation facet.

Occipital region (Pl. IIB). The large, more or less circular opening to the braincase (the *occipital foramen*) is a dominant feature in the caudal view of the skull. Ventral to the foramen lies the caudad facing circular *vertebrad concavity*. The caudo-ventrad, medio-ventrad facing oval *vertebrad facet* (condylus exoccipitalis, GOEDEL, 1974a) (Fig. 10) is found lateral-dorsal to the vertebrad concavity. The facet is supported by a short strut: the *vertebrad pillar* (Fig. 10). Half-way around the lateral margin, the occipital foramen bears the ventrad-laterad directed *vertebrad process*. Just rostral and lateral to the line connecting the vertebrad process and vertebrad facet, the *spino-occipital nerve foramen* opens caudad-laterad.

The caudal and occipital part of the supraoccipital crest (the *wing of the supraoccipital crest*) is thinner than the main and rostral body. This wing extends from a semicylindrical surface of which the dorsal margin of the occipital foramen is the base: the *supraoccipital semicylinder*. Lateral to the semicylinder the *occipital oval* is found. It is a flat dorsocaudad facing surface, bordered dorsally by the horizontal caudal edge of the supratemporal area, laterally by the epiotic pillar.

Ethmoidal region (Fig. 12). The *vomerine wing* is a laterad extension of the rostrad continuation of the parasphenoid bar. The wing starts at the rostral end of the parasphenoid ventral crest, and runs latero-rostrad. In transverse section the space between left and right wing is a ventrad open triangle (the *subvomerine fossa*, Pls IC & IIA). This fossa reaches its greatest depth rostrally and here it is sealed off by what can be described as a rostrad curved rim (the *vomerine rim*, Pls IC & IIA). The lateral face of the rim is indented (the *vomerine notch*). In lateral view this notch is horn-shaped in out-line, the tapering part of the horn is caudo-dorsad curved. The caudal margin of the notch abuts against the *vomerine palatinad articulation facet* which faces dorso-caudad, laterad-caudad. From the top of the notch the lateral-dorsal margin of the ethmoidal region runs dorso-caudad for its greater part. Caudally, however, it curves laterad to meet the preorbital process. Halfway along its rostrad-caudad part the margin bears the laterad facing *mesethmoidal palatinad articulation facet*. Just rostral to the curving point the lateral-dorsal margin bears the small *palatinad protuberance*. The *vomerine lateral fossa* is surrounded by the vomerine palatinad

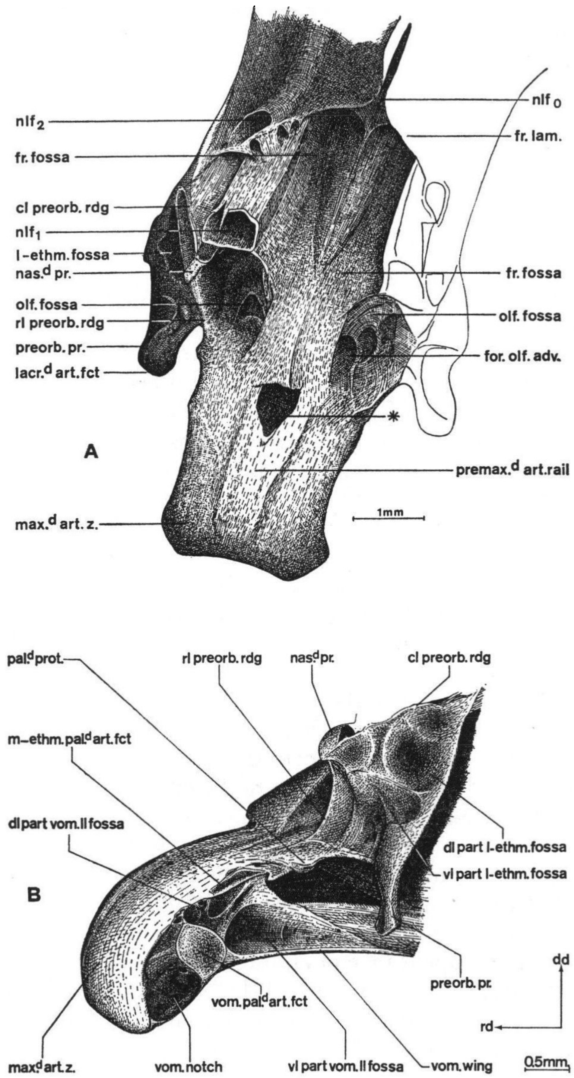


Fig. 12. Ethmoidal region of the neurocranium. A: dorsal face. Rostral-dorsal, medial-dorsal view. The asterisk marks the hole left after maceration of the cartilagenous plug which supports the premaxillad articulation rail caudally. B: lateral view.

articulation facet, the mesethmoidal palatinad articulation facet and the vomerine wing. The rostral part of this fossa is divided into a *dorsal* and a *ventral part.*

Starting from the nasad process (see p. 183), two ridges can be distinguished: 1. the *rostral preorbital ridge* running rostro-ventrad to the palatinad protuberance; 2. the *caudal preorbital ridge* running caudad-laterad to the edge of the orbital margin (see p. 183). Between these ridges and laterad the corresponding part of the orbital margin the *lateroethmoidal fossa* is found. A transverse ridge divides the fossa into a *dorsal* and a *ventral part.*

Medial to the rostral preorbital ridge the *olfactory fossa* is situated. The caudal wall of this fossa forms a rostrad facing concavity, its dorsal border is the floor of NLF_1. The foramen olfactorium advehens (see p. 185) opens in the medial-ventral corner of the fossa's caudal wall. The medial part of the ethmoidal dorsal surface is continued caudad as the floor of the broad *frontal fossa* (rostral fossa of LIEM, 1970). Although this fossa really belongs to the orbital region, it is, for practical purposes, described in the present section. The rostral part of the fossa is open dorsally. Caudad it is gradually overarched by the left and right *frontal lamella*, extending mediad from the left and right dorsal margin of the lateral walls of the fossa. The lamellae originate at the level of NLF_2 as mediad ridges of little transverse depth and converge caudad. They meet at the rostral origin of the supraoccipital crest. Here the unpaired NLF_0 (coronal pore: BRANSON, 1961) (Pl. IA) is found. Caudal to this point the fossa is left and right continued as a blind ending tube, medially separated by the intracranial foundation of the supraoccipital crest.

For its main part the dorsal surface of the ethmoidal area is relatively flat and rostro-dorsad facing. Sagittally on the dorsal surface the *premaxillad articulation rail* is found as an inconspicuous rounded ridge. Rostrally the dorsal surface curves sharply ventrad, terminating on the rostral face of the vomerine rim (see p. 190). This rounded aspect of the rostral part of the ethmoidal region gives the skull of *Haplochromis elegans* the typical appearance of ending in a knob-like blunt nose (the *ethmo-vomerine block:* GREENWOOD, 1974) (Pl. IA). The lateral surface of this "nose" is interrupted by the vomerine notch (see p. 190). The *maxillad articulation zône* is situated on the latero-rostral face of the ethmo-vomerine block.

Suspensorial apparatus (Figs. 13–20)

Suspensorium (Figs. 13–17)

Orientation and outline (Figs 13 & 14). Five peripheral articulation

facets and their curved, interconnecting lines are used in describing the suspensorial outline in its most extensive view. The finger-shaped maxillad process (see p. 194) is rostral-dorsally situated. It bears the maxillad articulation facet on its tip. At the rostral-ventral corner of the suspensorium the hourglass-shaped mandibulad articulation facet (see p. 198 is found. The caudal-dorsal corner of the suspensorium lodges the remaining three facets. The rostral and caudal neurocraniad condyles (see p. 199) are dorsally; the operculad condyle (see p. 199) lies caudo-ventral to the caudal neurocraniad condyle.

The plane through the mandibulad facet and the neurocraniad condyles is the relative sagittal plane. A major part of the suspensorial outline is smoothly excurved. This excurvation is the external border of the preopercular flange (see p. 201). On the lateral side of the suspensorium, four from the seven suspensorial lateral line foramina open on the internal border of this preopercular flange. The *suspensorial lateral line foramina (SLF)* are numbered 1–7 in a dorsal-ventrad-rostrad order (see p. 201). The line connecting SLF_2 and the tip of the maxillad process defines the relative horizontal direction.

The dorsal outline between the maxillad process and rostral neurocraniad condyle is incurved ventrad, U-shaped and is referred to as the *eye border*.

The short sections of the suspensorial outline from the rostral to the caudal neurocraniad condyle, and from the caudal neurocraniad condyle to the operculad condyle are called the *neurocraniad* and *operculad intercondyle border* respectively. Lateral to the neurocraniad intercondyle border the freely exposed mainly dorsad directed *preopercular top* is found. It terminates in the dorsad facing SLF_1. The gap between the base of the preopercular top and the pillar supporting the rostral neurocraniad condyle is bridged by the *hyomandibular transverse edge*. The rostral and caudal border of the preopercular top are continued ventrad as two diverging lines. These lines delimit the *preopercular vertical limb*. Ventrally they curve rostrad forming the *preopercular horizontal limb*. Together the limbs form the characteristically L-shaped figure on the cheek of the intact fish. The external margins of the limbs make up the major part of the caudal and ventral border of the suspensorium. The *rostral border* is the suspensorial outline between the mandibulad and maxillad articulation facet. From the mandibulad articulation facet to the maxillad one three sectors, of approximately equal length may be distinguished running vertical, rostro-dorsad and mainly horizontal respectively.

The suspensorial regions (Fig. 13B). In lateral view three regions are distinguished: the *palatine region* which lies rostral to a vertical line

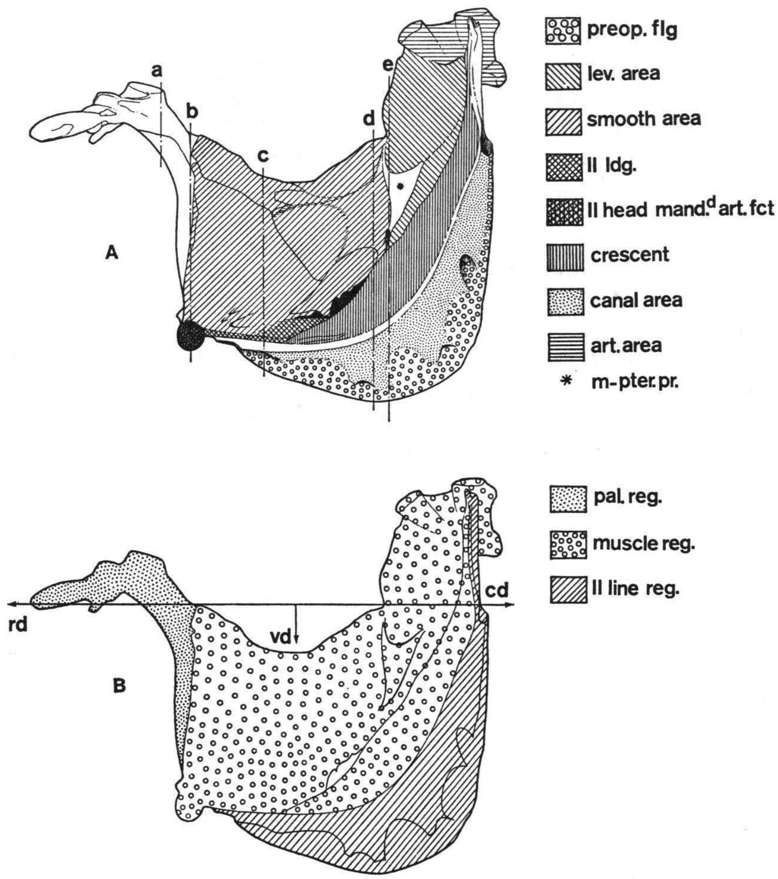


Fig. 13. Left suspensorium. Lateral view. The lines through A mark the approximate places of the transverse sections figured in 14B.

through the mandibulad facet, the *lateral line region* formed by the preopercular limbs and finally the *muscle region.*

The palatine region (Figs 15 & 16): As a slightly laterad curved finger-shaped process, the *maxillad process* extends away from the main suspensorial plane in a latero-rostrad direction. A small protuberance on the latero-dorsal face at the caudal origin of the maxillad process is called the *saddle-knob*. The knob bears a conspicuous flat face which faces mainly rostrad-dorsad to a saddle-shaped excavation on the

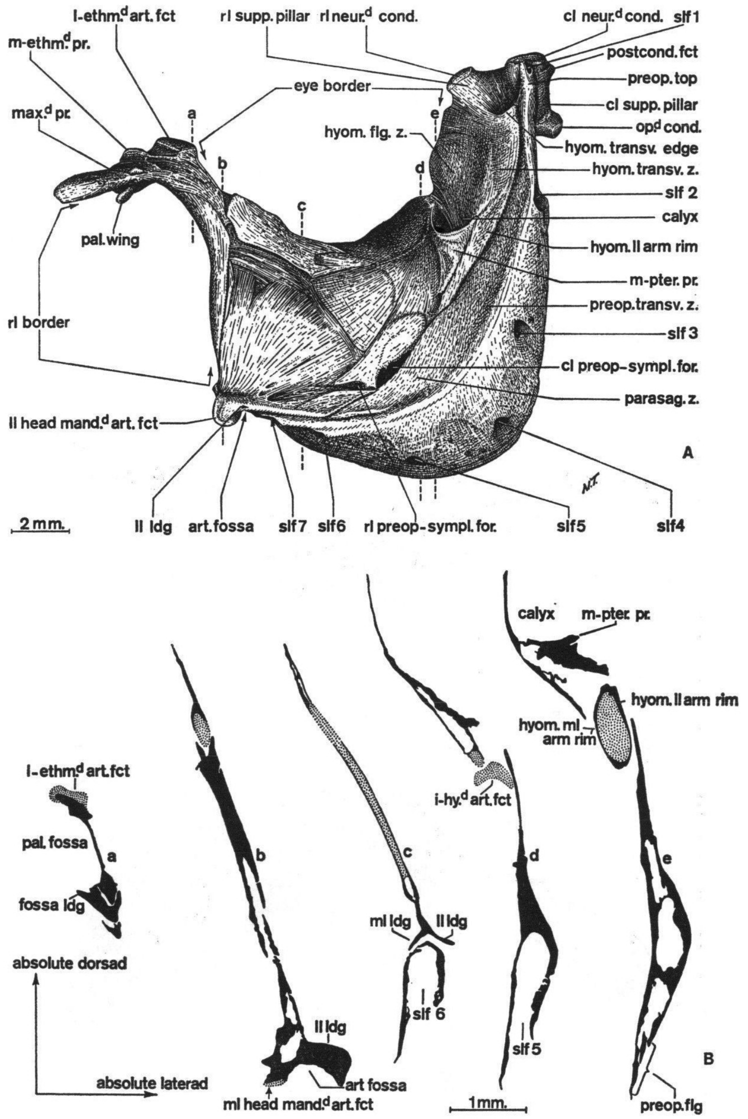


Fig. 14. A: left suspensorium Lateral view. B: absolute transverse sections through a suspensorium, approximately at the levels indicated in A and Fig. 13A. The sections are derived from serial-sections of a complete head in a non-expanded situation.

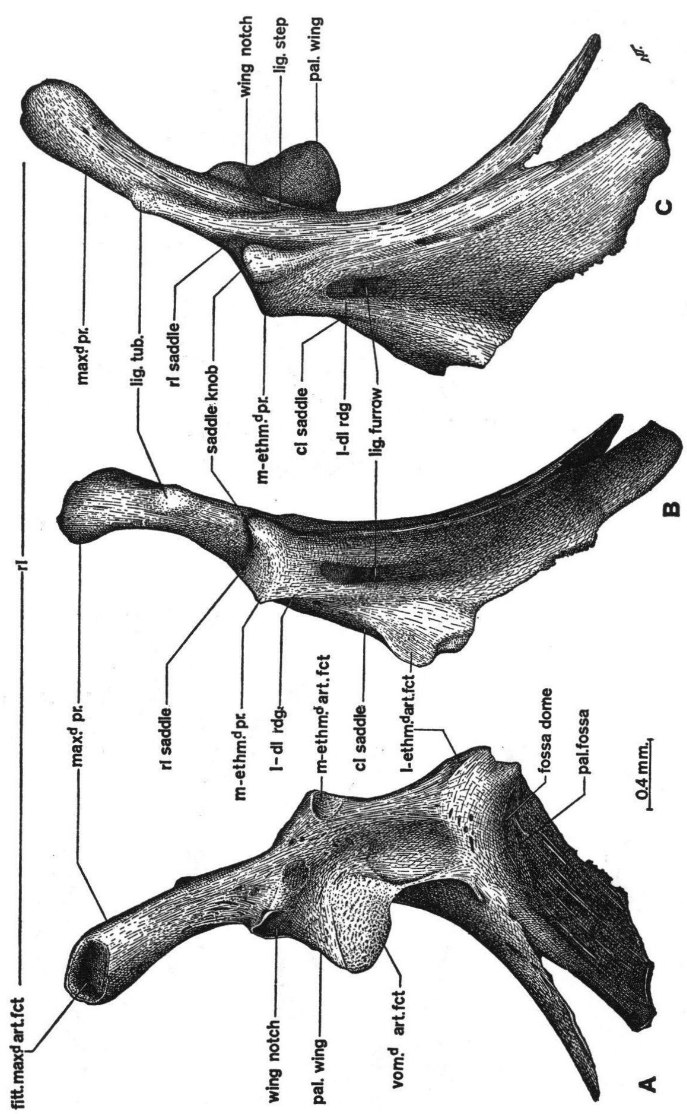


Fig. 15. Palatine of the right suspensorium. Palatine and ectopterygoid together constitute the palatine region of the suspensorium. A: medial-ventral view. B: latero-dorsal view. C: ventro-lateral view.

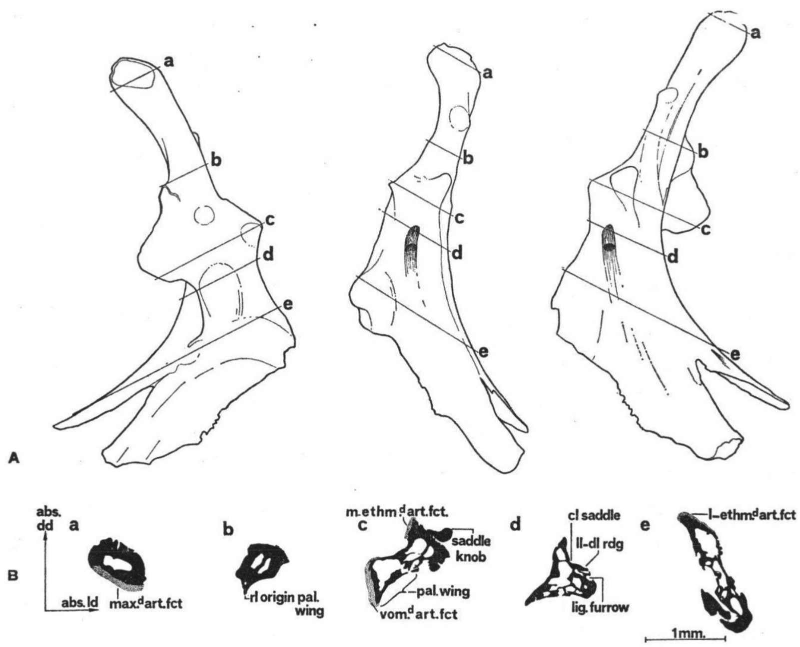


Fig. 16. Absolute transverse sections through the palatine. The sections are derived from serial-sections of a complete head in a non-expanded situation. The sections are made approximatively at the levels indicated in the outline drawings. The outline drawings are based on Fig. 15.

dorsal part of the palatine region (the *rostral saddle*). The ventral face at a level of a transverse section through the saddle-knob is step-like interrupted: the *ligament step*. On the lateral face of the maxillad process near the lateral-rostral corner of the rostral saddle, an inconspicuous projection is found: the *ligament tubercle*. It borders the compressed part of the maxillad process caudally. Compared to the gently sloping rostral wall of the rostral saddle, the caudal wall is steep. Dorsally this caudal wall contributes to the *mesethmoidad process*. From the top of the mesethmoidad process a small ridge descends along the latero-dorsal face of the palatine region: the *latero-dorsal ridge*. This ridge is the lateral margin of the *caudal saddle* and the dorsal margin of a laterad facing furrow (the *ligament furrow*).

Caudally the horizontal part of the rostral border (see p. 193) bears the medio-ventrad *palatine wing*. The rostral wall of this wing is indented: the *wing notch*.

On the medial side of the suspensorium lies the ***palatine fossa*** in the

dorso-caudal corner of the palatine region as a mainly ventrad facing scalloped part protected on three sides. The rostral border of the fossa is elevated into the mediad protruding *fossa-ledge* whose course approximately coincides with the rostro-dorsad section of the rostral border. Ventrally the ledge curves caudad and joins a horizontal series of mediad protuberances (the *insertion protuberances*, not figured) which lie ventral to the horizontal part of the eye border (see p. 193). Dorsally the fossa ends in a ventrad facing dome-shaped impression: the *fossa dome*.

The palatine region carries four articulation facets:

1. On the rostral tip of the maxillad process and extending for a short distance on the medio-ventral face, lies the *maxillad articulation facet*.
2. The medial face of the mesethmoidad process (see p. 197) bears the concave, mediad facing *mesethmoidad articulation facet*.
3. Caudal to the caudal saddle (see p. 197), the dorsal border of the palatine region is dorsad elevated and bears the *lateroethmoidad articulation facet*.
4. The spherical-triangular mediad facing *vomerad articulation facet* occupies the medial side of the rostral-ventral corner of the palatine wing.

The muscle region (Figs 13, 14 & 17). The *mandibulad articulation facet* resembles an asymmetrical hourglass with a mainly transverse directed longitudinal axis. The mandibulad articulation facet consists of the smaller *medial head* and a large *lateral head*, leaving the constriction in the suspensorial sagittal plane. Caudal to the mandibulad facet and rostral to the tip of the preopercular horizontal limb a ventrad facing concavity is situated: the *articulation fossa*. Caudal to the fossa the medial aspect of the suspensorium reveals the mediad opening horicontal *symplectic-quadrate groove*. The flat floor of the groove is called the *medial ledge*; its dorsal covering is the *symplectic ridge*. Rostrally the medial ledge bears a protuberance on its medial margin: the *ledge-process*. The lateral head of the mandibulad facet is supported caudally by the well-developed caudad running horizontal *lateral ledge*. Near the caudal ends of the medial and lateral ledge the suspensorium is perforated by two foramina: the *rostral* and *caudal preopercular-symplectic foramen*. Ventral to the rostral preopercular-symplectic foramen the lateral ledge narrows mediad. Here the *preopercular crescent* begins. The external border of the crescent consists of the curved part of the internal border of the lateral line region and the straight, vertical part of that border dorsally as far as the level of the hyomandibular transverse edge (see p. 193). Internally the crescent is bordered by an incurved line, ending and beginning at the same points as the external border and partly exposed as a sharp edge, partly as a groove. A

ventral part of the internal border forms the ventral edge of the caudal preopercular-symplectic foramen. Caudally in the preopercular crescent, the vertical, elongate *preopercular transverse zone* can be distinguished from the remaining mainly *parasagittal zone*.

Latero-caudad to the caudal, vertical part of the eye border (see p. 193), a thin lamella extends as far as the dorsal part of the preopercular vertical limb (the *levator area*). The dorsal border of the levator area consists of the supporting pillar of the rostral neurocraniad condyle and of the hyomandibular transverse edge (see p. 193). The larger rostral zone of this levator area is rostro-laterad facing and called the *hyomandibular flange zone*. The smaller rostrad facing caudal part of the levator area is the *hyomandibular transverse zone*. Ventrally the hyomandibular flange zone ends in the hyomandibular lateral arm-rim (see below) and in a dorsad facing, ventrad tapering pocket: the *calyx*. The lateral wall of the calyx is the *metapterygoid process*. The *hyomandibular lateral arm-rim* is exposed between the caudal border of the calyx and the internal border of the preopercular crescent. Its medial opposite is the *hyomandibular medial arm-rim*. The rims slope rostro-ventrad. On the medial face of the suspensorium, the medial rim terminates ventrally as the caudo-dorsal border of a conspicuous mediad facing depression: the *interhyad depression* of which the lateral and dorsal border form the *interhyad articulation facet*. On the medial face, opposite the levator area, a large foramen opens rostro-dorsad: the *hyomandibular foramen* (not figured).

The muscle area caudad to the hyomandibular transverse zone is the *articulation area*. The rostrad-dorsad directed *rostral supporting pillar* bears the rostrad-dorsad facing *rostral neurocraniad condyle*. In contrast to the protruding spherical rostral condyle, the *caudal neurocraniad condyle* is elipsoid, with a rostrad-caudad long axis, faces dorsad and has little vertical depth. This caudal condyle is supported by the *caudal supporting pillar* which, especially on medial view, appears as a short rostrad curved cylinder. On the dorsal face of the caudal pillar the *postcondyle facet* is found caudal to the neurocraniad condyle. Ventrally the caudal pillar bears the spherical, ventro-caudad facing *operculad condyle*. The caudal face of the caudal supporting pillar is the operculad intercondyle border (see p. 193).

The last part distinguished in the muscle region is the *smooth area*, bounded rostrally by the palatine region, ventrally by the lateral ledge, caudally by the preopercular crescent and the metapterygoid process, dorsally by the horizontal part of the eye border. Compared to the other areas, its surface is relatively smooth, without sharp directional changes, ridges etc. Its rostral-ventral zone is parasagittal, but dorsally, especially caudal-dorsally, it arches mediad.

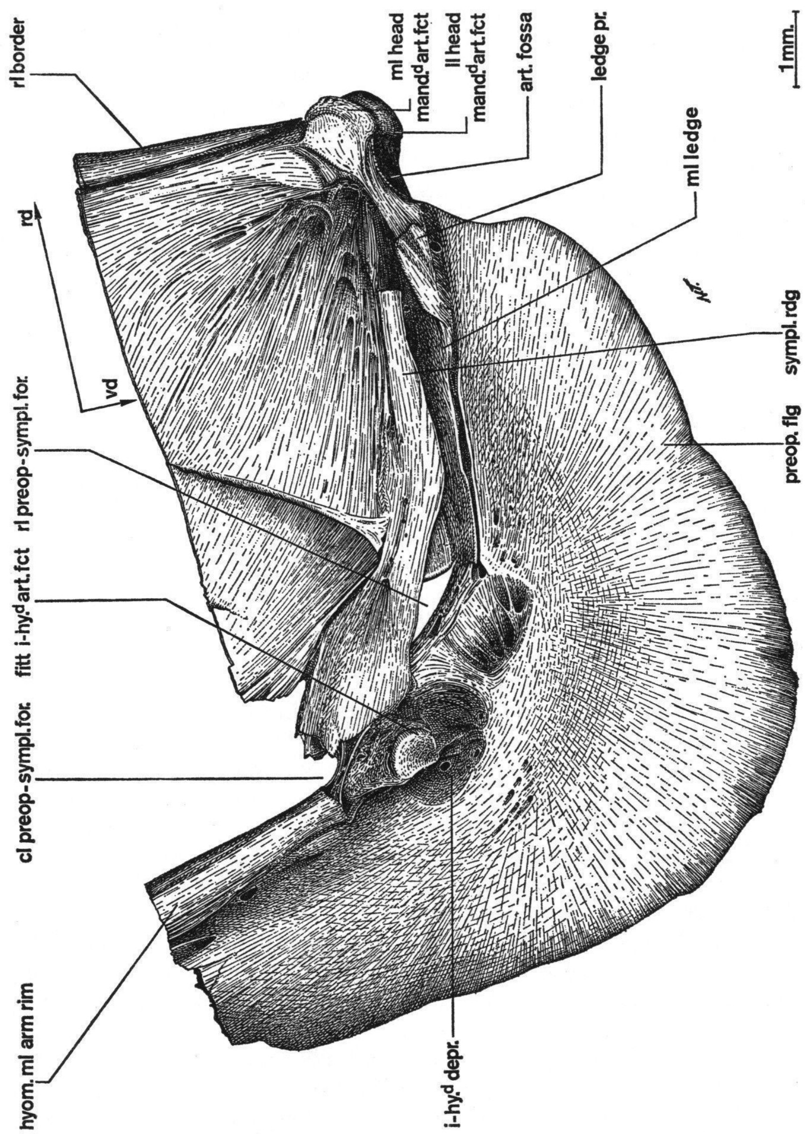


Fig. 17. Ventral part of left suspensorium. Medial view.

The lateral line region. Except for the preopercular top, this region bears externally the thin, parasagittal directed *preopercular flange.* The remaining, internal area is called: the *canal-area.* By definition the preopercular top belongs to the canal-area. Seven foramina *(SLF_{1-7})* open from the canal area. *SLF_1* opens dorsad at the preopercular top. *SLF_2* opens rostrad at the rostral termination of the horizontal limb. *$SLF_{4,5}$* are situated in the ventral-caudal corner of the flange. *SLF_1* opens caudad-ventrad, *SLF_5* ventrad. The latter being the largest of the 7 foramina. *$SLF_{4,5}$* are characteristically connected to the main canal by short canaliculi. *$SLF_{2,3}$* are smaller, caudad facing openings on the caudal margin of the vertical part of the canal area. *SLF_2* is near the dorsal origin of the preopercular flange. *SLF_3* lies more or less halfway between SLF_2 and SLF_4. The rostro-ventrad facing *SLF_6* opens from the ventral margin of the horizontal part of the canal area, $^1/_3$ from its rostral origin between SLF_7 and SLF_5.

Gill-cover (Figs 18 & 19)

The gill-cover is a thin, lamellar, slightly concave element, approximately triangular in outline. The main plane through the element is the sagittal one. The concavity faces mediad. One of the sides of the triangle is, for its greater part, reinforced by a ridge which projects laterad: the *suspensoriad ridge.* The suspensoriad ridge terminates at the vertex of the triangle which is extended into a process: the *dilatator*

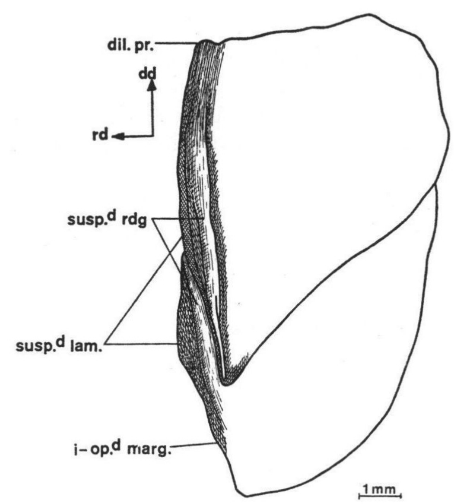


Fig. 18. Left gill-cover. Lateral view.

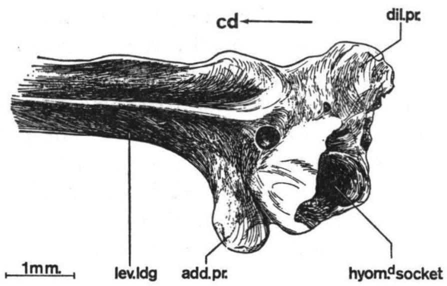


Fig. 19. Rostro-dorsal corner of left gill-cover. Medio-dorsal view.

process. This vertex lies on the rostral-dorsal corner; the long axis of the suspensoriad ridge runs, by definition, ventrad-dorsad. The suspensoriad ridge covers the dorsal three quarters of the rostral margin of the gill-cover, leaving the ventral quarter (the *interoperculad margin*) free. The *suspensoriad lamella* is a sagittal flange rostral to the suspensoriad ridge. Its best developed part is the rostrad excurved ventral half.

The dorsal margin of the gill-cover is straight and nearly perpendicular to the rostral one. The ventro-caudal margin of the gill-cover bears two excurvations, the ventral excurvation being most pronounced.

At the medial side of the gill-cover a complex of socket, process and ledge is discerned in the rostro-dorsal corner. The *suspensoriad articulation socket* is a hemispherically shaped, medio-rostrad facing concavity ventral to the dilatator process. Caudal to the socket, the nearly horizontal *levator ledge* is found. Halfway along the horizontal length of the gill-cover this ledge gradually merges into the general level of the medial surface. Rostrally the ledge turns mediad to form the *adductor-process* which lies just caudal-medial to the socket wall.

Interoperculum (Fig. 20)

The interoperculum is a flat oblong element with the tapering end deeply notched: the *ligament notch*. The plane through the element

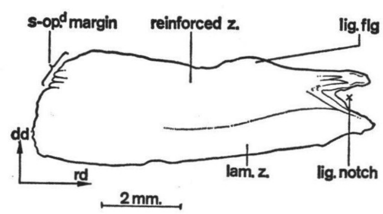


Fig. 20. Right interoperculum. Lateral view.

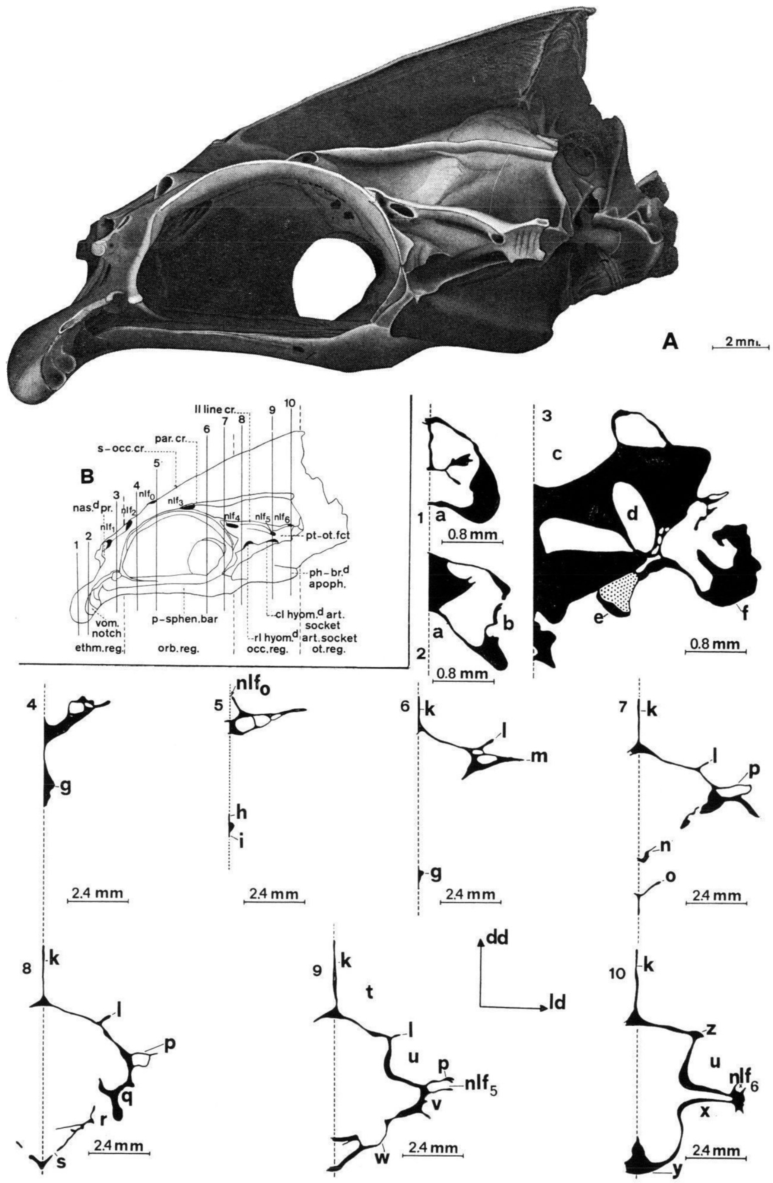
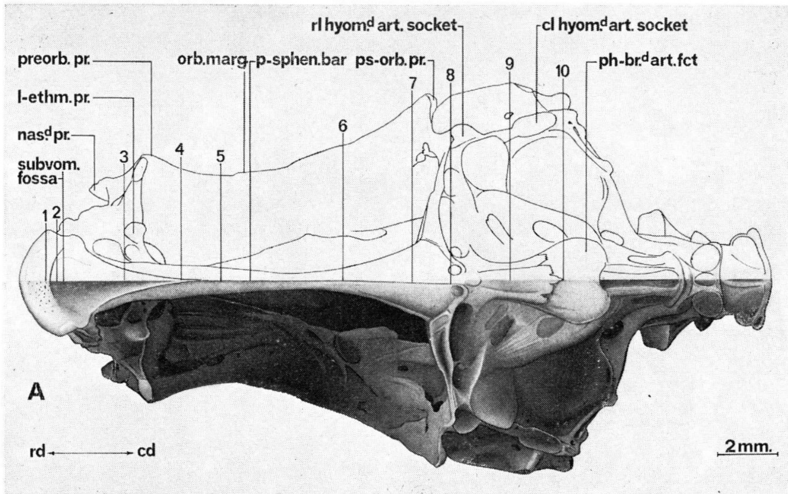


Plate I. Neurocranium. A: lateral view; B: outline based on A; C: transverse sections derived from serial sections of a complete head. The level of the sections is indicated approximately in B and in Pl. IIA. a: subvomerine fossa, b: vomerine notch, c: frontal fossa, d: foramen olfactorium advehens, e: lateroethmoidal palatinad articulation facet, f: preorbital process, g: parasphenoid bar, h: parasphenoid dorsal crest, i: parasphenoid ventral crest, k: supraoccipital crest, l: parietal crest, m: orbital margin, n: basisphenoid wing, o: parasphenoid wing, p: lateral line crest, q: rostral hyomandibulad articulation socket, r: chamber-floor foramen, s: carotic foramen, t: supratemporal area, u: temporal area, v: dilatator area, w: otic bulla, x: lateral awning, y: pharyngobranchiad articulation facet, z: epiotic process.



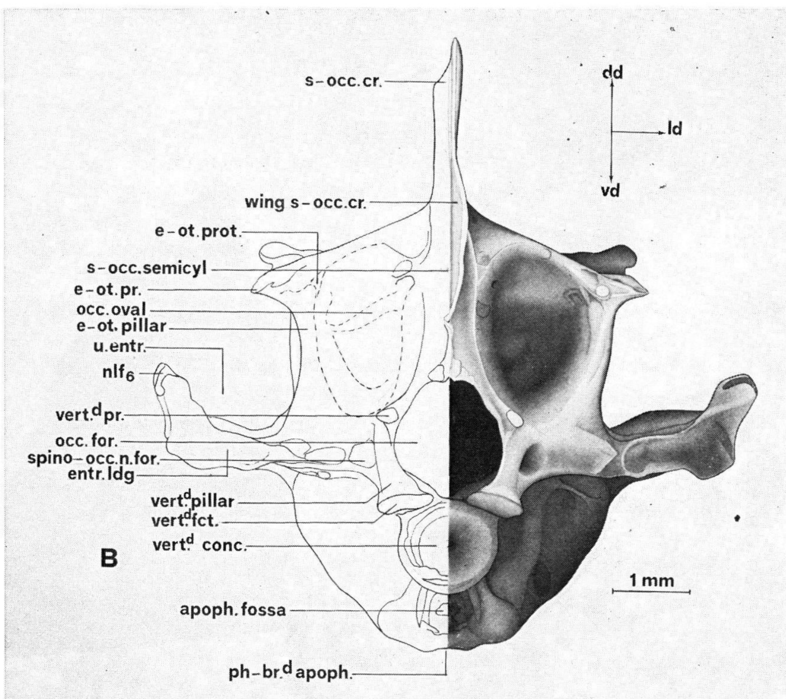


Plate II. Neurocranium. A: ventral view. The lines through the figure indicate the approximate levels of the sections figured in Pl. IC. B: caudal view.

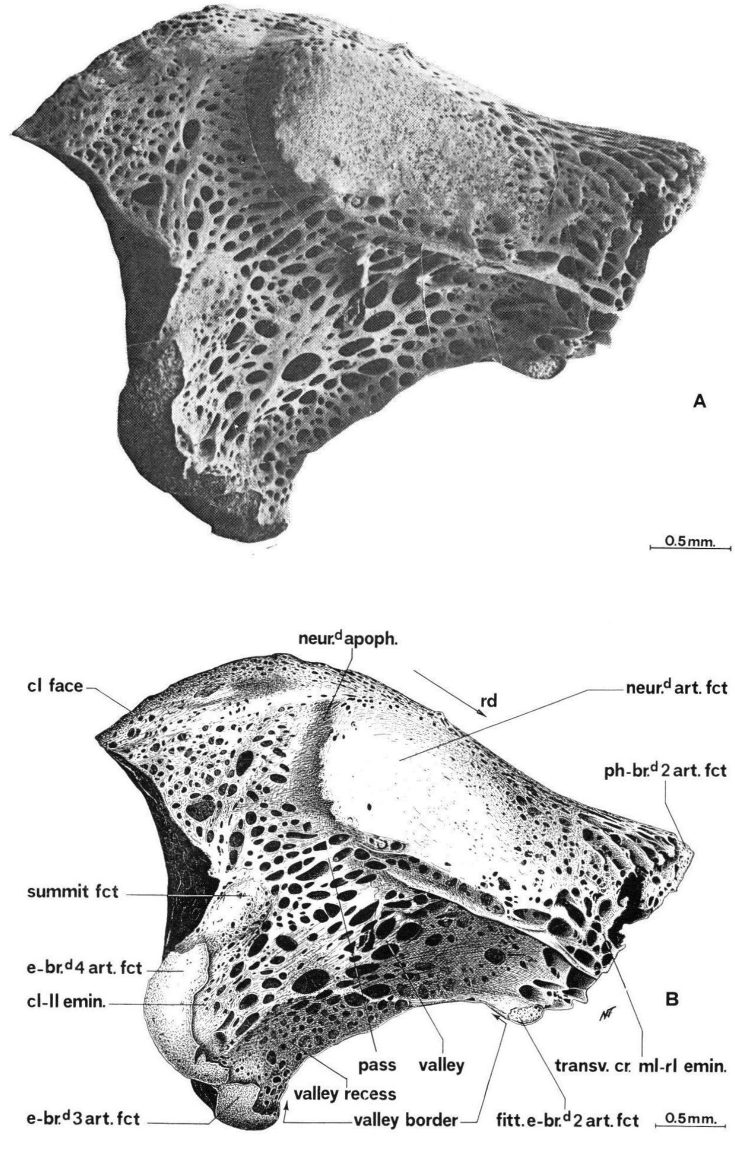


Plate III. Pharyngobranchial 3 region of the right pharyngobranchial 3,4. Laterodorsal view. A: collage of seven stereoscan-photo's. For nearly all figures in the present paper similar photo-collages have been prepared. B: drawing based on A and on observations on the preparation self.

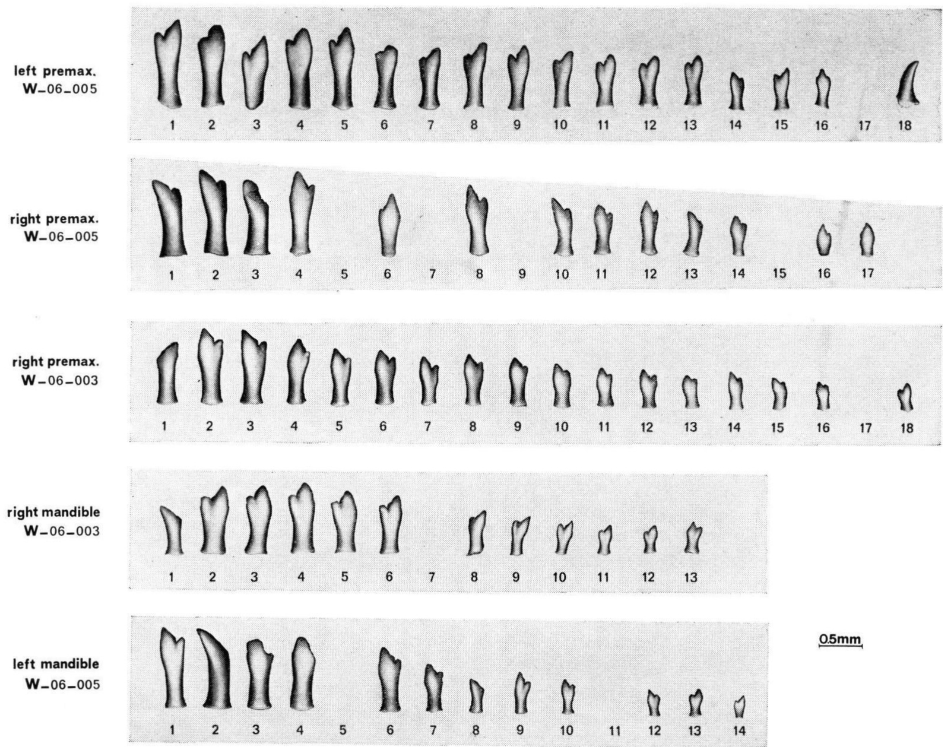
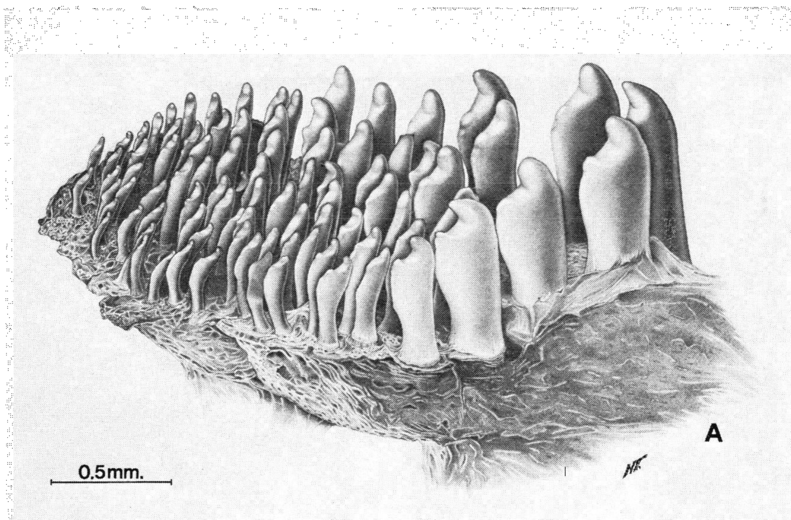


Plate IV. Jaw teeth of wild adult specimens. View on the sagittal planes of the teeth. The plate shows the variation in tooth-shapes found in wild *H. elegans*. The teeth are numbered from medial-rostral to caudal. Teeth from open places were lost during preparation.



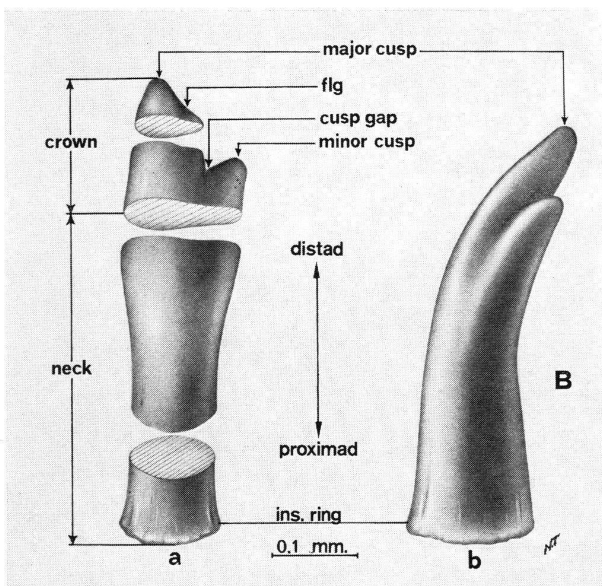


Plate V. A: teeth on the right pharyngobranchial 3,4. Caudal-medial, ventro-medial view. The figure demonstrates the various tooth-shapes found among the pharyngeal teeth. B: typical flange-bearing jaw-tooth. a: view on the sagittal plane, b: view on the transverse plane.

defines its sagittal plane, the notch lies rostrally and the line through the straight and ventral side runs, by definition, rostrad-caudad. Ventrally the element is thinner in cross-section than dorsally. This thin part is referred to as the *lamellar zone*, the thicker dorsal part as the *reinforced zone*. The ligament notch is a reentrant angle penetrating into the reinforced zone. Dorso-caudally the reinforced zone terminates in spinules: the *suboperculad margin*.

Intraspecific variation is observed in the degree of curvature of the interopercular dorsal border but the rostral second quarter is always exposed as a flange-like dorsad excurvation: the *ligament flange*.

Jaw apparatus (Fig. 21–24)

Mandible (Figs 21 & 22)

Lateral aspect (Fig. 21A & B). In its most extensive aspect the mandibular outline approaches a triangle. The triangular outline is, however, interrupted by two large fissures. The largest penetrates from the (dorsal) vertex of the triangle: the *dorsal obturated foramen* (foramen obturatum, GOEDEL, 1974a following LUBOSCH, 1929), the smaller one interrupts the opposite (= ventral) base of the triangle: the *ventral obturated foramen*. The lateral aspect is marked by a horizontal series of lateral line foramina along the ventral margin. The rostral oblique side of the triangle is, for its greater part, provided with teeth. The tooth-bearing face of the mandible is referred to as the *dentigerous area*. Descriptions of tooth-shapes are dealt with on pp. 227–229.

The dorsal obturated foramen is rostrally bordered by an excurved line. The line converges with another one to form the acute *reentrant angle* which opens caudad. The ventral arm of this angle defines the rostrad-caudad directions. The *coronoid process* is the dorsal zone of a dorso-caudad directed wing-like process: the *coronoid wing* (processus coronoideus, GOEDEL, 1974a, following LUBOSCH, 1929). The *primordial process* (GOEDEL, 1974a, following LUBOSCH, 1929) is the reinforced caudal margin of the mandible running caudoventrad from the entrance of the dorsal obturated foramen to the conspicuous bipartite *suspensoriad articulation facet* (see below). The facet is bordered laterally by the hemicircular *lateral facet rim*. From this rim and dorsal to the horizontal arm of the reentrant angle, the *articular excurvation* is found, an elongate surface eminence excurved laterad on transverse section which tapers rostrad in the reentrant angle. Between the articular excurvation and the primordial process the *articular web* is spread out. Its incurved free edge forms the caudal and ventral border of the dorsal obturated foramen.

The *dental recess* is a shallow impression rostrally in the lateral face

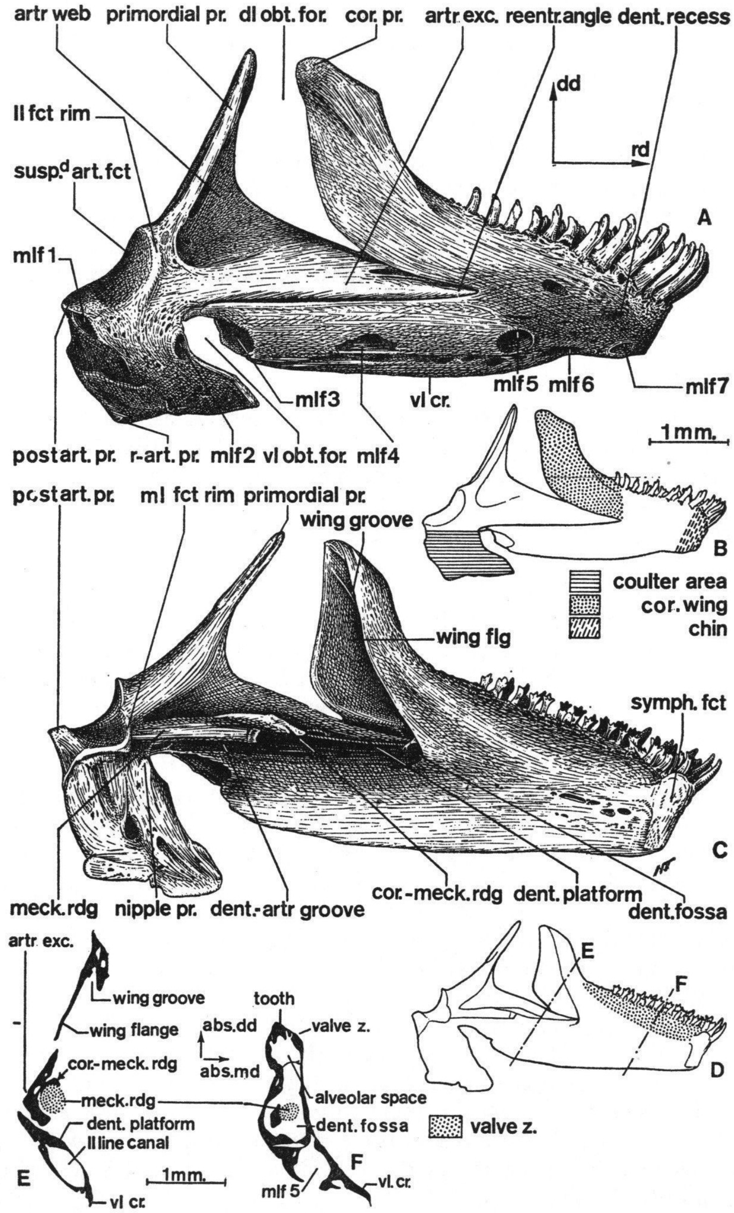


Fig. 21. Mandible. A: right mandible. Lateral view. C: left mandible. Medial view. From the meckelian ridge only the bone-fitting is left. The rostral, cartilaginous part was lost during maceration. E, F: absolute transverse sections derived from serial-sections of a complete head in a non-expanded situation. The sections are approximatively at the levels indicated in D.

where this face curves mediad-rostrad. The mandibular area rostral to this recess is the *chin.*

In the ventral margin of the mandible a horizontal series of usually 7 lateral line foramina is found, numbered MLF_{1-7} in a caudal-rostrad order. $MLF_{6,7}$ are smaller and more ventrally situated than $MLF_{4,5}$. MLF_7 lies in the chin zone and is sometimes very small or even absent. $\mathrm{MLF}_{4,5}$ open laterad-ventrad, at least more laterad than the mainly ventrad facing $\mathrm{MLF}_{6,7}$. MLF_3 opens caudad into the ventral obturated foramen. At the opposite side of the foramen the rostrad facing MLF_2 is found. Finally MLF_1 opens caudad, ventral-caudal to the suspensoriad articulation facet. Between MLF_6 and MLF_3 the ventral margin is projecting as a medio-ventrad directed crest. the *ventral crest.* The mandibular area ventrad to the line connecting the dorsal margins of MLF_1 and $_2$ somewhat resembles a coulter and is therefore referred to as the *coulter-area.* The caudal border of this area lies between two caudad directed processes: (1) dorsally the *postarticulation process* which caps MLF_1 dorsal-medially; (2) ventrally the *retroarticular process* which forms the mandibular caudal-ventral corner.

Medial aspect (Fig. 21C & D). The medial face of the rostral margin of the coronoid wing is provided with the caudad opening *wing groove.* The extensive lamellar part of the coronoid wing between the rostral border of the dorsal obturated foramen and the ceiling of the groove is the *wing flange.* The wing groove is the caudo-dorsad continuation of the ceiling of the *dental fossa,* which penetrates rostrad deeply into the mandible. The floor of this fossa is the rostral part of the elongate, horizontal, rostrad running *dental platform* which extends caudad as far as MLF_3. Just dorsal to the platform and over its entire length the *meckelian ridge* protrudes from the medial face of the mandible, leaving the *dento-articular groove* between platform and ridge. Dorsally on the middle third of the medially visible part of the meckelian ridge, the elongate triangular *coronomeckelian ridge* (sesamarticulare, GOEDEL, 1974a) is found. The *nipple process* is a blunt dorsad protuberance on the medial side of the coulter-area near MLF_2. The medial border of the suspensoriad articulation facet forms a rim: the *medial facet rim.*

The *valve zone* is an elongate section on the medial side just ventral to the dentigerous area. Contrasting to the remaining parts of the medial face ventral to the dentigerous area, the valve zone has a definite dorsad component in its facing vector. It follows the mediad curving rostral end of the mandible which terminates as the mediad facing *symphyseal facet.*

Caudal aspect (Fig. 22). The most complete view of the suspensoriad

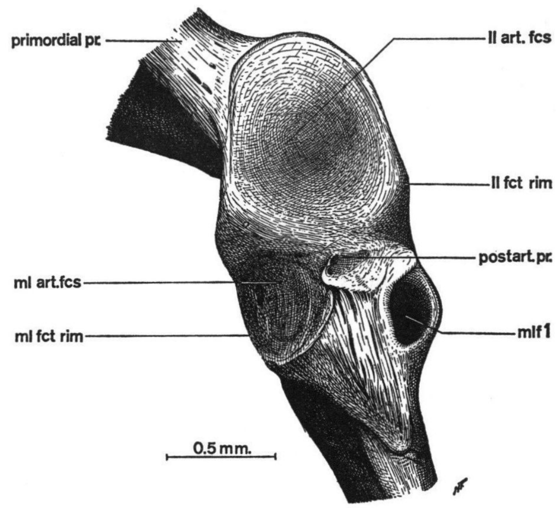


Fig. 22. Suspensoriad articulation facet of the right mandible. Caudal view.

articulation facet is gained from caudal. Ventral to the primordial process lies the larger of the two surfaces making up the facet. This *lateral articulation facies* is in outline an oval of which the lateral facet rim forms the lateral semicircular border. The abutting *medial articulation facies* is much smaller and faces caudo-mediad. Its medial border is the medial facet rim. The margin between both facies is caudad continued as the postarticulation process (Fig. 21).

Premaxilla (Fig 23B & C).

Outline and orientation (Fig. 23C). The premaxilla consists of two elongate arms, nearly perpendicular to each other. The *dentigerous arm* lies caudally to the ascending arm and is marked by a band of teeth, whose shape is discussed on pp. 227–229. The *ascending arm* runs dorsad-ventrad. The plane through the ascending arm and parallel to the straight, caudal part of the dentigerous arm defines the relative sagittal plane. Seen in dorsal view the rostral part of the premaxilla curves mediad.

Lateral aspect (Fig. 23C). The ascending arm terminates in two dorsad pointing processes. The rostral higher one is the *ascending spine*; the caudal one is the very short *maxillad spine*. The two processes are interconnected by the ventrad incurved sharp *interprocess edge*. Dorsad

this edge is continued as the caudal border of a parasagittal ridge along the ascending spine: the *ascending ridge*. A caudad facing, vertical groove (the *ascending spine groove*) is exposed between the ascending ridge and the rostral symphyseal ridge (see below). Two foramina are marked in the lateral face: 1. the *dorsal external face foramen* opens latero-dorsad ventrally to the maxillad spine and 2. the *ventral external face foramen* opens laterad in the rostral-ventral corner of the lateral face. Except for a short rostral part, the dentigerous arm bears dorsally the *dentigerous arm ridge*.

Medial-caudal view (Fig. 23B). Except for a short dorsal part of the ascending spine, the mediad facing, vertical *symphyseal groove* is found over the entire vertical depth of the ascending arm. The groove is bordered rostrally and dorsally by ridges: the *rostral symphyseal ridge* and the *caudal symphyseal ridge* respectively. In its ventral half the caudal symphyseal ridge broadens with a caudad excurvation. This broader part of the ridge forms the medial facing oblong *symphyseal articulation facet*.

Ventral to the maxillad spine a vertical, elongate articulation facet faces caudad: the *maxillad articulation facet*. Ventrally the facet dilates somewhat and becomes bullate. Between this articulation facet and the symphyseal articulation facet, a shallow vertically running depression is found: the *interfacet depression*. In caudal view the interprocess edge appears to be the dorsal border of a thin lamella (the *fossa lamella*) which rostrally borders the deep, dorsad opening *fossa*. The floor of the interfacet depression forms the medio-caudal wall of this fossa.

Rostral cartilage (Fig. 23A).

The rostral cartilage resembles a drip or a four sided pyramid of which the point directs dorsad. The plane of symmetry is the sagittal plane.

In cross section about halfway along its vertical length, all sides are incurved and one incurvation is definitely longer than the others. This side belongs to the *rostral face*. The opposite side is the *neurocraniad articulation facet*. This neurocraniad facet is saddle-like curved: incurved on horizontal section, excurved on sagittal section. The lateral faces and the ventral face form a continuous gutter-like impression: the *marginal incurvation*.

Maxilla (Fig. 24).

The maxilla is a rather elongate element of which one end consists of four large processes protruding in various directions, whereas the

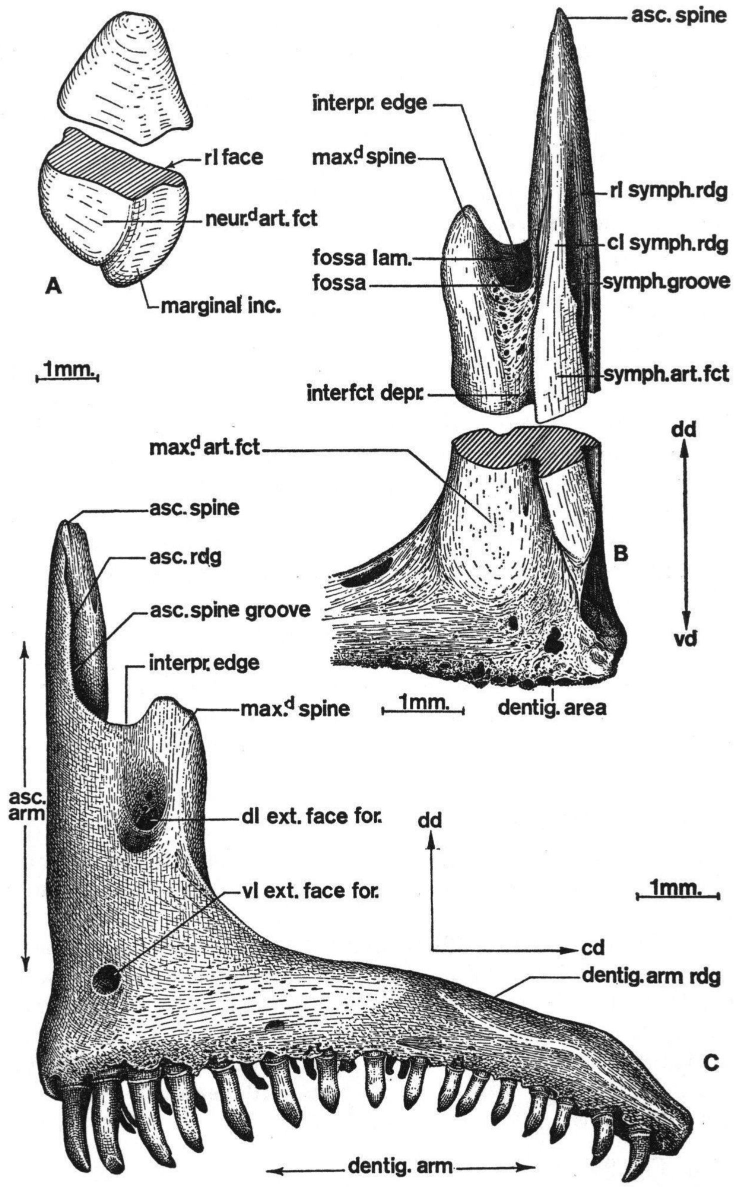


Fig. 23. Rostral cartilage and left premaxilla. A: rostral cartilage. Caudal-lateral view. B: premaxillary ascending arm. Medial-caudal view. C: premaxilla. Lateral view. Note the unicuspid teeth typical of overgrown specimens. The premaxilla belonged to a specimen of 97 mm standard length.

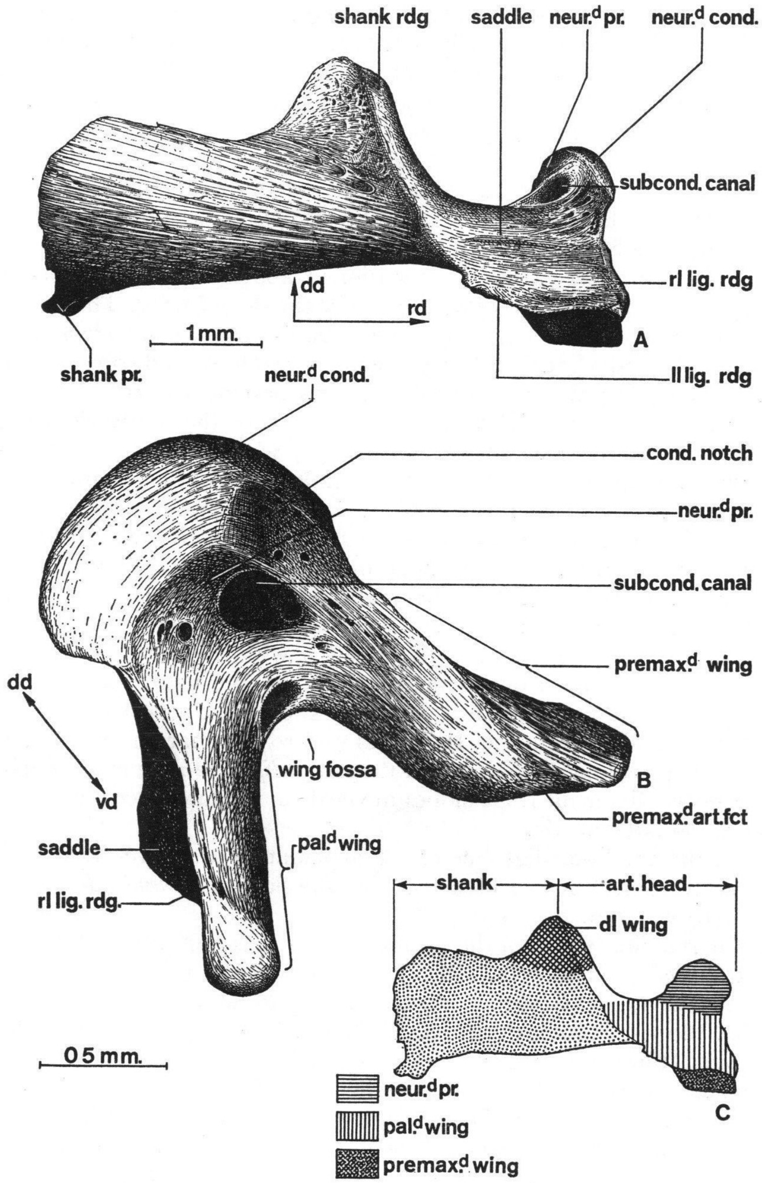


Fig. 24. Right maxilla. A: mainly lateral view. B: medial-rostral view of the articulation head. C: outline based on A.

other end is relatively flat. The latter end forms the main part of the shank of which a topologically more precise definition is given below. The plane of the shank is the relative sagittal plane. The ventral long side of the shank is reinforced and straight. It runs, by definition, rostrad-caudad. The process-bearing end lies rostrally. In cross-section the outline of the caudal part of the shank is curved laterad. On the medial face of this curved part the *shank-foramen* opens. Caudal-ventrally the shank terminates in the *shank process* which shape varies intraspecifically.

Of the four large processes mentioned above, two direct dorsad: rostrally the *neurocraniad process*, caudally the dorsal wing. The neurocraniad process bears dorsally and caudal-medially the *neurocraniad condyle*: a semicylindrical surface with a caudo-dorsad curved long axis. The plane through the condyle-axis and neurocraniad process faces mediad-rostrad. Through the process runs the *subcondylar canal.* The *dorsal wing* is a thin sagittal flange, with an excurved dorsal border. On the lateral face of the maxilla the rostral margin of the dorsal wing appears to be reinforced: the *shank ridge*. This ridge marks the border between the *shank* and the *articulation head*. The shank ridge is continued ventrally as the caudal margin of the large latero-ventrad directed *palatinad wing*. The dorso-lateral face of this wing is flat and faces dorso-laterad, rostro-laterad. The *saddle* is defined as this dorso-lateral face of the palatinad wing together with the ventrad incurved part of the maxilla's dorsal margin between the neurocraniad condyle and the top of the dorsal wing. In its broadest aspect, the saddle is quadrangular in outline. Its lateral and rostral margin are referred to as the *lateral ligament ridge* and the *rostral ligament ridge* respectively. The rostral ligament ridge slopes upwards to the lateral corner of the neurocraniad condyle.

On the caudo-medial face of the articulation head, ventral to the incurved, dorsal border of the saddle, the horizontal *tendon ledge* (not figured) is found.

The remaining part of the articulation head is best discussed from a rostral-medial view (Fig. 24B). From the neurocraniad process two ventrad diverging wings are observed. The lateral one is the palatinad wing, the medial one the *premaxillad wing*. The *wing fossa* is included between these two wings. The premaxillad wing directs rostrad-mediad, ventro-rostrad and bears the concave oval *premaxillad articulation facet* on its rostral-lateral face. The rostral-medial face of the neurocraniad process bears an opening of the subcondylar canal and is notched in its medial-dorsal corner (the *condyle notch*). The notch also interrupts the neurocraniad condyle.

Branchial apparatus (Plate III; Figs 6, 7, 25–35)

Pharyngobranchial 1 (Figs 4B & 6).

Pharyngobranchial 1 is a stick-like mediad-laterad flattened element of which the long axis defines the relative dorsad-ventrad directions. The broadest part of the element is the ventral side. The ventro-rostral zone bears the sagittal *ridge*. Dorsally and ventrally the element terminates in the *neurocraniad* and *epibranchiad 1 articulation facets* respectively.

Pharyngobranchial 2 (Fig. 25 & 35).

The main plane of this flat element defines the relative transverse plane. The *dentigerous area* is the mediad-laterad elongated, narrow, ventral face. Its teeth are discussed on p. 231.

The *rostral face* of pharyngobranchial 2 is a flat rostrad facing surface. The *caudal face*, on the other hand, is incurved, especially in a lateral-dorsal zone, where the lateral margin protrudes caudad. This protrusion bears the caudo-dorsad facing triangular *epibranchiad 2 articulation facet* on top. The medial-dorsal corner is excurved and lodges the narrow elongate *medial articulation facet.* The dorsal half of this medial facet forms the *epibranchiad 1 part*, the medial half the *pharyngobranchiad 3 part.* Between the lateral margins of the epibranchiad 2 articulation facet and of the dentigerous area, the *lateral face* appears as a mainly laterad, slightly rostrad facing surface with an overhanging dorsal part.

Pharyngobranchial 3, 4 (Pl. III; Figs 26, 46–49).

Pharyngobranchial 3, 4 and the lower pharyngeal element are the two largest elements in the branchial apparatus .Compared with the relatively dorsad-ventrad flattened lower pharyngeal element, pharyngobranchial 3, 4 is a rather lumpy element. The conspicuous tooth-bearing face (the *dentigerous area*) is flat, the opposite face being undulated. The dentigerous area defines the relative horizontal plane and faces ventrad. It has an ovoid outline with rostrally a rather acute end. The shapes of the teeth are dealt with on p. 231.

No less than six facets may be distinguished on the dorsal surface of pharyngobranchial 3, 4. These facets are concentrated on two eminences which give the dorsal surface its complexly undulating aspect. The largest and most conspicuous facet is the *neurocraniad articulation facet*, ventrally supported by the *neurocraniad apophysis*. The neurocraniad articulation facet is a large tongue-shaped surface on the medial part of the dorsal face. The longitudinal axis of the facet defines

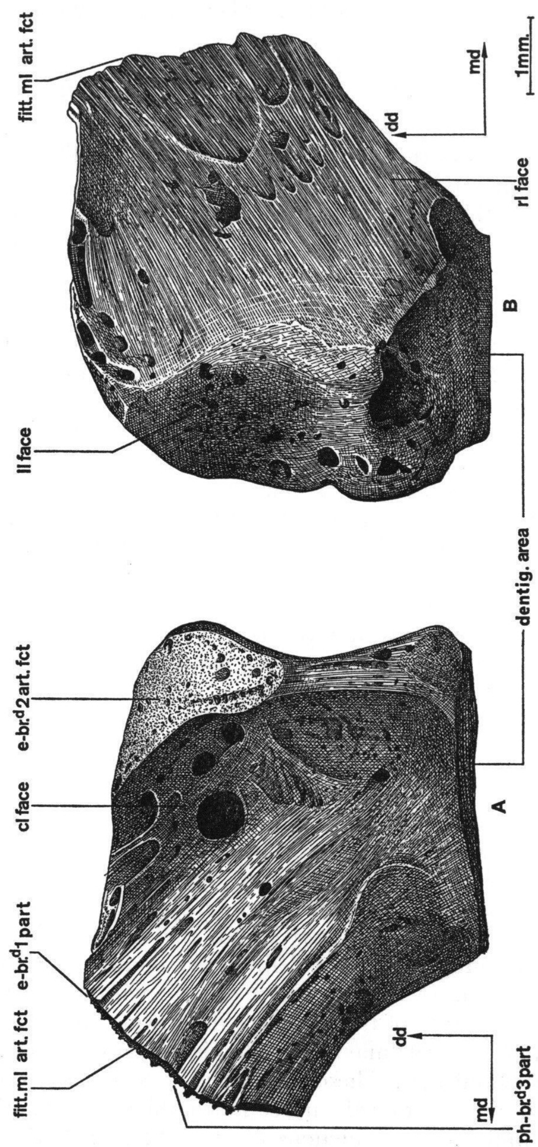


Fig. 25. Right pharyngobranchial 2. A: caudal view. B: latero-rostral view.

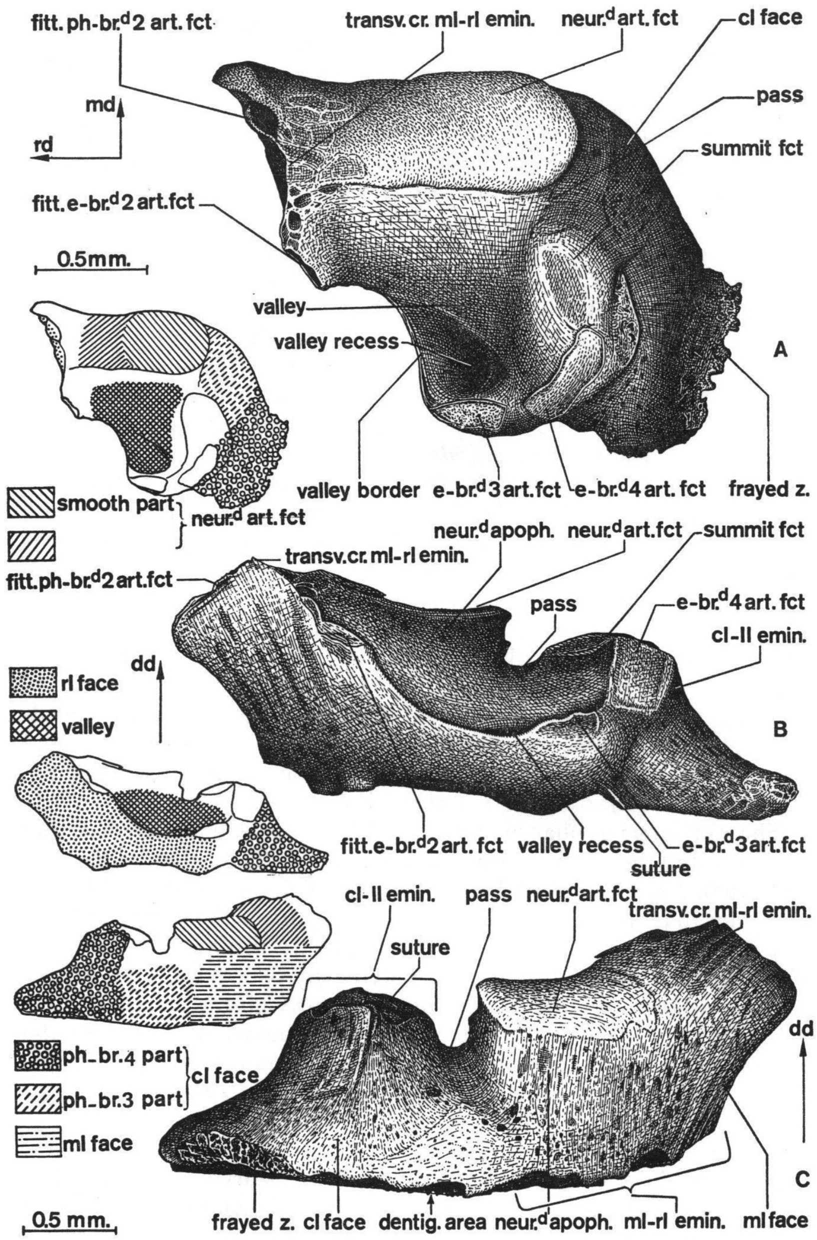


Fig. 26. Left pharyngobranchial 3,4. A: dorsal view. B: rostro-lateral view. C: caudal-medial view.

the rostrad-caudad directions. The neurocraniad apophysis and articulation facet form the major part of the highest elevation of pharyngobranchial 3, 4: the *medial-rostral eminence*. The remaining part of this eminence is the sharp *transverse crest* which forms part of the rostral-dorsal border of the element and from which the neurocraniad articulation facet starts medially. This crest bears an articulation facet, both on its medial and on its lateral corner: the *pharyngobranchiad 2 articulation facet* and the *epibranchiad 2 articulation facet* respectively.

The *caudal-lateral eminence* is found on the lateral half of pharyngobranchial 3,4, approximately halfway along its rostral-caudal length. Its summit lies centrally on the dorsal surface. From this summit the ridge of the emince slopes laterad-ventrad. The ridge is provided with facets which are not always clearly separated from one another. Often three facets can be distinguished. In a medial-laterad order these are referred to as: the *summit facet*; the *epibranchiad 4 articulation facet* and the *epibranchiad 3 articulation facet*.

Between the two eminences stretches the *valley*. From its incurved sharp rostral border (the *valley border*), between the epibranchiad 2 and 3 articulation facets, the floor of the valley slopes gently upwards to the relatively narrow *pass* between the summit of the caudal-lateral eminence and the caudal-lateral corner of the neurocraniad apophysis. The pass leads to the caudal face (see below). Medial to the epibranchiad 3 articulation facet the bottom of the valley has a depression: the *valley-recess*.

Between the rostral border of the dentigerous area and the rostral-dorsal border connecting the epibranchiad 3, epibranchiad 2 and pharyngobranchiad 2 articulation facets, the slightly overhanging, steep, ventro-rostrad facing *rostral face* is exposed.

The *medial face* of pharyngobranchial 3, 4 is steep, faces mediad and lies ventral to the medial border of the neurocraniad articulation facet. The *caudal face* is the caudal and medial declivity of the caudal-lateral eminence. The lateral half of the excurved part of the caudal margin of pharyngobranchial 3,4 is typically frayed: the *frayed zone* (crista pharyngobranchialis, GOEDEL, 1974b). Partly over the caudal face of the caudal lateral eminence and medially through the eminence runs the mainly transverse *suture*. It terminates somewhat medial to the frayed zone and divides pharyngobranchial 3,4 into the rostral *pharyngobranchial 3 region* and the caudal *pharyngobranchial 4 region.*

Epibranchial 1 (Fig. 27).

Epibranchial 1 resembles a Y with a slightly curved long axis. The plane through the arms of the Y defines the relative horizontal plane with the longitudinal axis of the short, *rostral arm* pointing mediad and

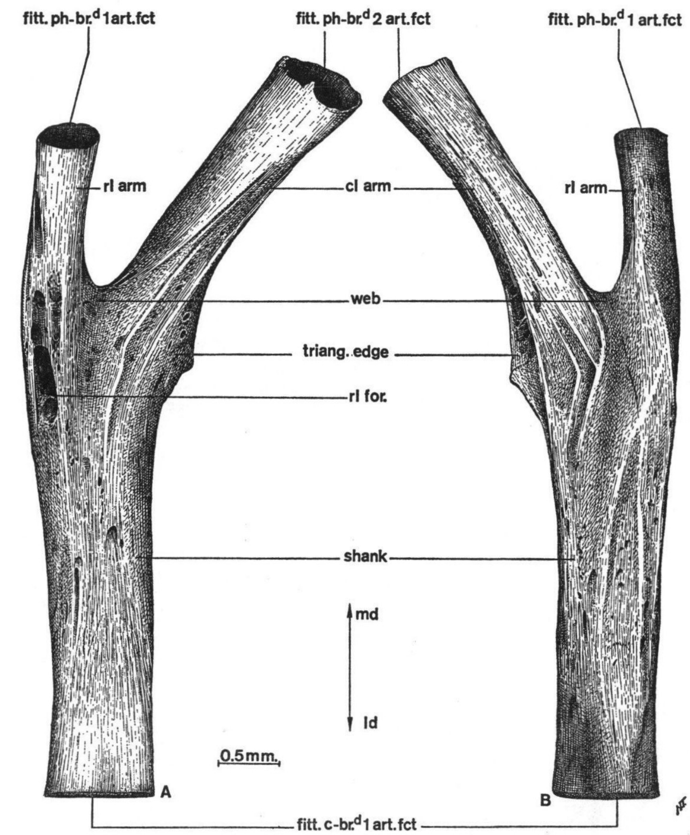


Fig. 27. Right epibranchial 1. A: ventral view. B: dorsal view.

the *shank* directing ventro-laterad. The remaining arm is the *caudal arm*. In transverse section the element is slightly curved in the transition zone between the arm to the shank. Between the arms a relatively thin *web* is spread over a short lateral sector. Besides the large *rostral foramen* in the middle third of the rostral face, numerous smaller foramina are observed especially ventrally in the zone where the arms and the shank meet. The caudal-dorsal margin bears the horizontal *triangular edge* in the transition zone from arms to shank. In some specimens the edge is inconspicuous. Arms and shank bear articulation facets terminally. The rostral arm ends in the *pharyngobranchiad 1 articulation facet*, the caudal arm in the *pharyngobranchiad 2 articulation facet*. The shank bears the *ceratobranchiad 1 articulation facet*.

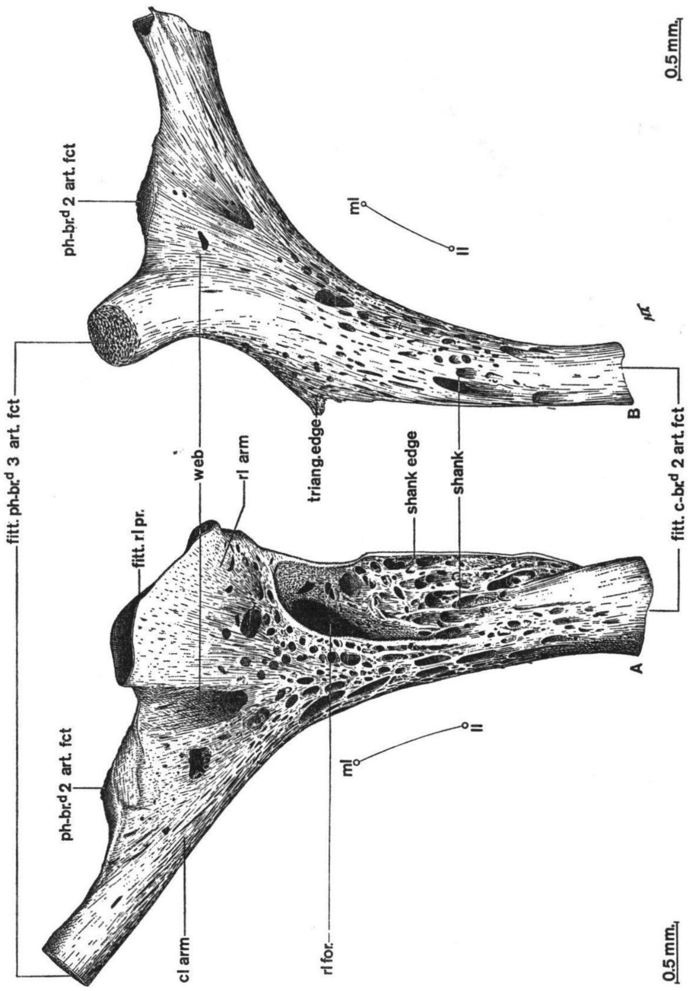


Fig. 28. Left epibranchial 2. A: medio-ventral, rostral-ventral view. B: medio-ventral, caudo-ventral view. As the figures are based on a macerated skeletal preparation, the conspicuous rostral process is lacking. For a complete impression of the form one should compare this figure with Fig. 6.

Epibranchial 2 (Fig. 28).

After comparison with epibranchial 1, epibranchial 2 may also be described as a curved Y. In epibranchial 2, however, the space between the arms is completely filled with the relatively thin *web*. The *pharyngobranchiad 2 articulation facet* is found as a small facet on the free margin of the web between the arms. The *rostral process* is a conspicuous flat mediad extension of the rostral arm (fig. 6). The *pharyngobranchiad 3 articulation facet* lies at the end of the caudal arm. The *ceratobranchiad 2 articulation facet* forms the termination of the ventro-laterad directed shank of the Y. The plane through the arms and the web forms the relative horizontal plane, the line connecting the ceratobranchiad and pharyngobranchiad 2 articulation facets runs transversely.

The caudal border is slightly incurved and bears at its midpoint the *triangular edge*, shaped like the corresponding edge in epibranchial 1.

Except for a short lateral part, the rostral-dorsal margin of the shank bears the rostrad extending *shank edge*. As in epibranchial 1 the *rostral foramen* is a conspicuous opening in the middle third of the rostral face. Numerous other and smaller foramina perforate the ventral face of epibranchial 2.

Epibranchial 3 (Fig. 29).

Epibranchial 3 bears two large and one smaller articulation facet. The plane through these facets is the relative transverse plane; the line connecting the larger facets runs mediad-laterad, the small facet lies dorsally.

In the epibranchial series one to three, epibranchial 3 may, for descriptional convenience, be looked upon as derived from the Y-shape of epibranchials 1 and 2. However, the shape and the lengths of the arms do differ greatly. The larger *ventral arm* is marked by the latero-ventrad protruding *spine*, corresponding with the triangular edges of epibranchials 1 and 2. The ventral arm terminates medially in the *pharyngobranchiad 3,4 articulation facet*. The smaller *dorsal arm* bears the *arm-facet* on top and on its dorso-medial corner the mediad facing *epibranchiad 4 articulation facet*. Based on the comparison with epibranchials 1 and 2, the *web* is distinguished between the dorsal and and ventral arms. Topologically similar to the preceding epibranchials, the *shank* of epibranchial 3 ends with the *ceratobranchiad 3 articulation facet*.

In a ventral view the long axis through the continuous shank and ventral arm is curved rostrad. On the ventral face, immediately lateral to the spine, an impression is found which is incurved dorsad

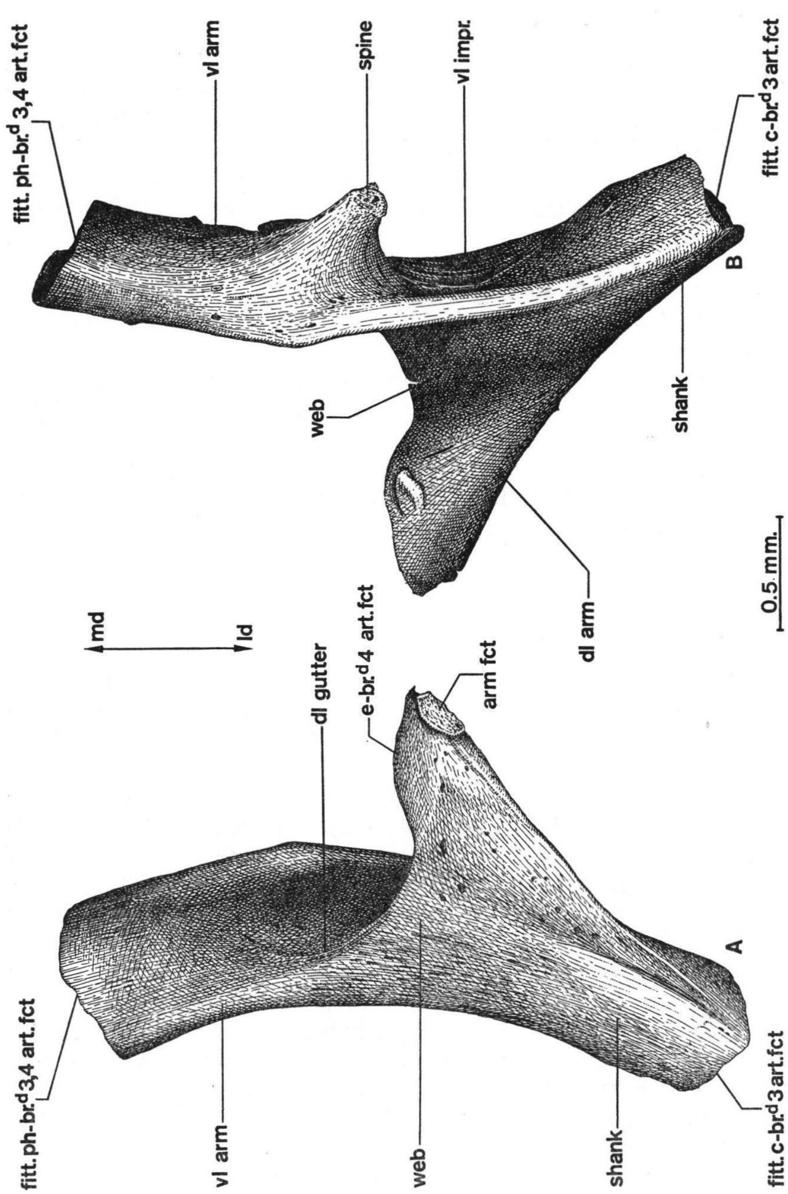


Fig. 29. Right epibranchial 3. A: caudal-dorsal view. B: ventro-rostral view.

on parasagittal section. This *ventral impression* narrows laterad and disappears laterally. The dorsal face of the shank and the ventral arm is, except for the lateral part of the shank, provided with a shallow gutter-like impression (the *dorsal gutter*) running laterad-mediad. The web borders the lateral half of the dorsal gutter rostrally.

Epibranchial 4 (Fig. 30).

As in epibranchial 3 two large and one small articulation facet are found on epibranchial 4. The plane through these facets lies horizontal. The line connecting the largest and smallest facets runs mediad-laterad, the second large facet lying caudally. Looking on the horizontal plane the element may be described as a quadrangle with a large shank attached to one of its corners. The *quadrangular region*

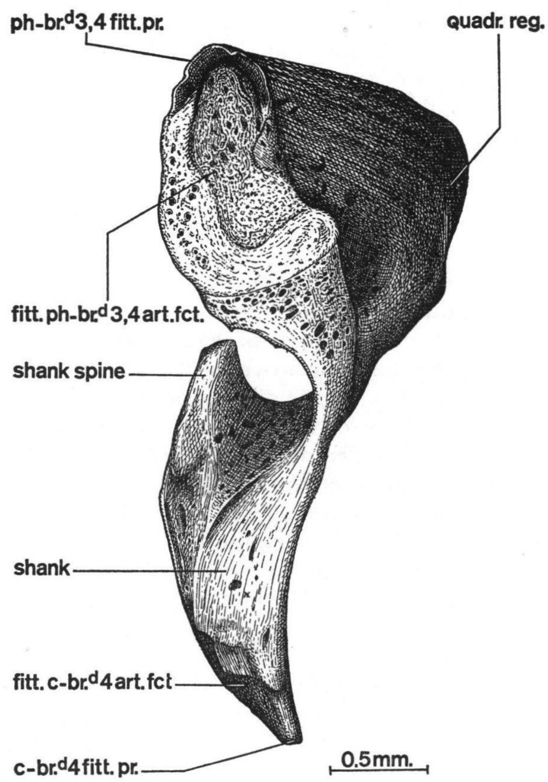


Fig. 30. Left epibranchial 4. Ventro-medial view.

lies medially. The *shank* is directed caudo-laterad and terminates in the *ceratobranchiad 4 articulation facet*. Dorsally the shank is produced into the well-developed dorso-mediad directed *shank spine*. The ceratobranchiad 4 articulation facet is protected rostrally by a laterad-caudad outgrowth of the rostral margin: the *ceratobranchiad 4 fitting process*. The shank is attached to the caudal-lateral corner of the quadrangular region. The long sides of the quadrangle are directed mediad-laterad. The greatest part of the quadrangular region is rather thin, but the caudal long side and the medial short side are thickened. The medial short side bears the *pharyngobranchiad 3,4 articulation facet*, rostrally capped by an extension of the rostral long side: the *pharyngobranchiad 3,4 fitting process*. The *epibranchiad 3 articulation facet* (fig. 6) is found on the short lateral side in the rostro-lateral corner of the element.

The general impression of the element is that of a twisted shape, whereby the quadrangular region has been turned away from the plane through the shank and the shank spine. The impression of torsion is strongest in the constricted part forming the transition from the shank to the quadrangular region.

Ceratobranchials 1–4 (Fig. 7)

The four ceratobranchials resemble each other in being slender, elongate, slightly curved elements, bearing an articulation facet at each end and a longitudinal groove on the ventral face (the *ventral gutter*). The longitudinal axis of the element runs, by definition, mediad-laterad. The medial part of each element broadens (the *dilation zone*), is somewhat dorsad-ventrad flattened and bears the *medial articulation facet*. The degree of dilation varies for each element. It is hardly discernable in ceratobranchial 1, observable in ceratobranchial 2. Besides this difference in dilation and the shorter length of ceratobranchial 2, no clear cut qualitative shape-differences between ceratobranchial 1 and ceratobranchial 2 were found. In ceratobranchial 3 the dilation zone is well-pronounced and provided rostrally with the ventrad *dilation ridge*. The medial half of this ridge is characteristically bevelled in a rostral view. The lateral half gradually merges into the rostral wall of the ventral gutter. The caudal wall of the ventral gutter is absent in the dilation zone of ceratobranchial 3.

Ceratobranchial 4 has a typical knife-like appearance in a dorsal view. The handle of the knife is the dilation zone and occupies about one third of the length of the element. The rostral margin of this zone forms the well-developed ventrad *dilation ledge*. Ventral to the medial articulation facet this ledge terminates in the sharp mediad pointed

medial spine. The *blade* of the knife is a flange extending caudad from the dorsal side of ceratobranchial 4.

The *epibranchiad 1–4 articulation facets* are finger-shaped processes on the non-dilated ends of the ceratobranchials. A cross-section at the medial end of the ceratobranchials will be approximately oval in outline; at the lateral end this outline is roundish or triangular. In ceratobranchial 4 the laterad protruding *lateral spine* is found dorsal to the epibranchiad 4 articulation facet.

Hypobranchial 1 (Fig. 31B).

The outline of the broadest aspect of hypobranchial 1 forms a quadrilateral figure with curved sides. The two longest sides are incurved and approximately parallel with the longitudinal, that is, relative transverse axis of the element. Each of the shorter and excurved sides bears an elongate articulation facet, the shorter of which is the *ceratobranchiad 1 articulation facet*. Its long axis runs, by definition, horizontally. The longer facet is the medially situated *copulad articulation facet* of which the long axis runs rostrad-ventrad. Because the facet-axes are not parallel, hypobranchial 1 gives the impression of a twisted plane. The ventral face is slightly incurved in cross-section. In a dorsal or ventral view the *rostral process* may be located by describing it as that part of the excurved, lateral side which is not occupied by the ceratobranchiad 1 articulation facet. In cross-section the outline of the rostral process curves somewhat ventrad. A small protuberance (the *caudal process*) is sometimes found as an interruption halfway along the caudal border.

Hypobranchial 2 (Fig. 31A).

In being shorter and broader, the general appearance of hypobranchial 2 is more stocky than that of hypobranchial 1 but topologically homologous parts can be discerned. In broadest aspect hypobranchial 2 can be described as a quadrangular body provided with an obtusely angled triangular flange (the *rostral process*) of which the base occupies the main part of a longer side of the quadrangle. This is the rostral side. The caudal long side is roughly parallel to the base of the rostral process and is definitely incurved. The line connecting the caudal corners runs, by definition, transversely. The two remaining, shorter, sides are approximately perpendicular to the transverse axis described before and each forms an elongate articulation facet. In contrast to hypobranchial 1, the *ceratobranchiad 2 articulation facet* of the second hypobranchial is the longer one. The long axis of the medially situated *copulad articulation facet* runs, by definition, horizontal. As in

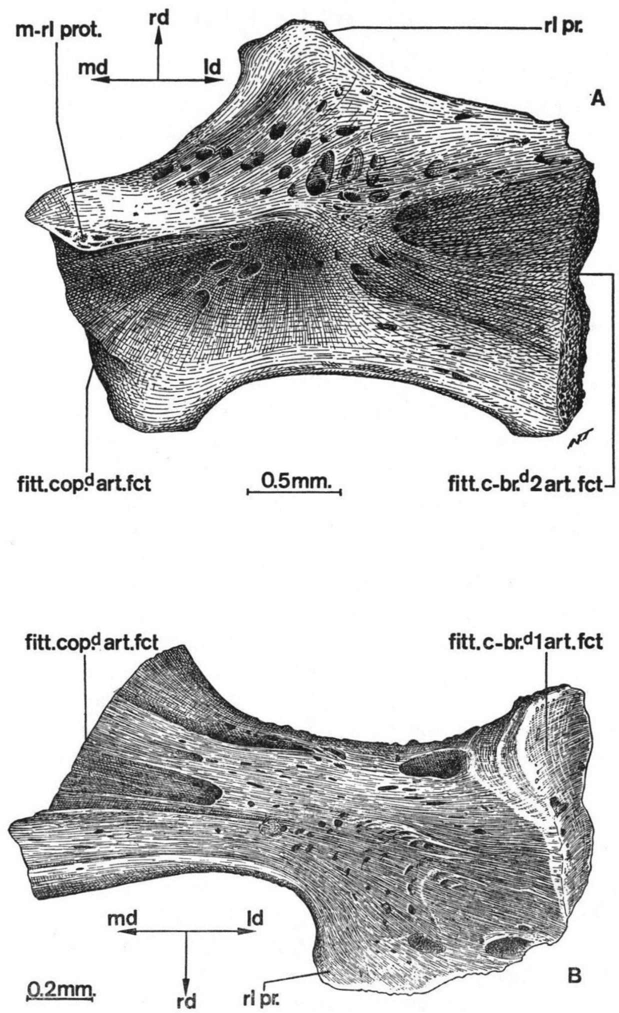


Fig. 31. A: left hypobranchial 2. Ventral view. B: right hypobranchial 1. Ventral view.

hypobranchial 1, the ventral face of hypobranchial 2 is slightly incurved in cross-section. Characteristic for the second hypobranchial is a ventrad protuberance on the medio-rostral margin between the rostral process and the copulad articulation facet: the ***medio-rostral protuberance***.

Hypobranchial 3 (Fig. 32).

The broadest aspect of hypobranchial 3 may be described as a scoop of which the *blade* has grown out asymmetrically mediad. The longi-

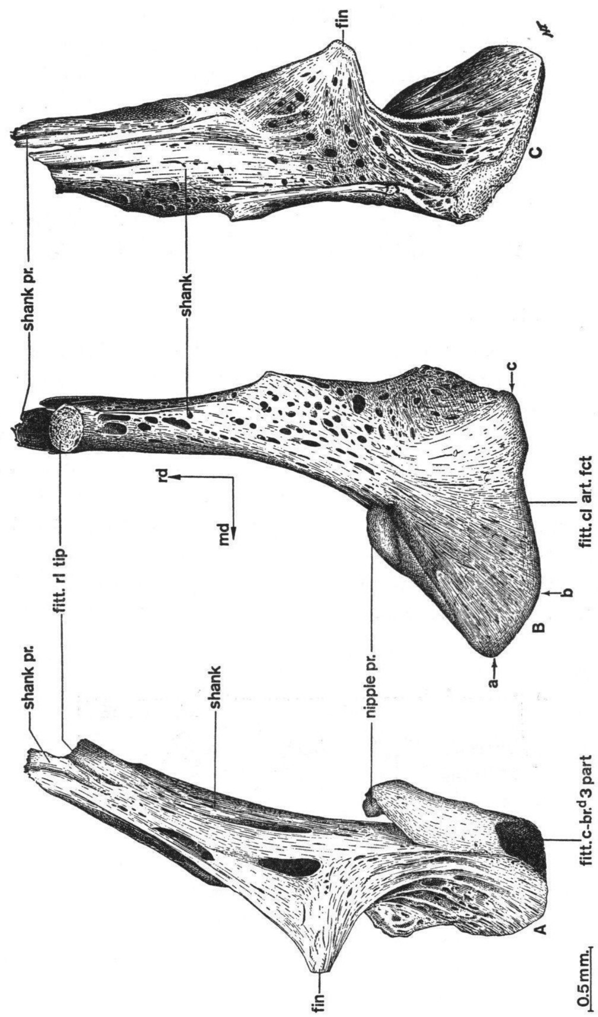


Fig. 32. Right hypobranchial 3. A: ventro-medial view. B: dorsal view. The caudal border between a–b comprises the central cartilaginad part of the caudal articulation facet. Between b–c lies the ceratobranchiad 3 part. C: ventro-lateral view.

tudinal axis of the *shank* directs rostrad. It is the ventral face of the shank that is medially provided with the ventrad directing, parasagittal *fin*. The fin is triangular in broadest view, the ventral point of the triangle lying at the level of the transition from shank to blade. The caudal and excurved side of the blade is provided with the extensive *caudal articulation facet*. The medial part of the caudal articulation facet is the *central cartilaginad part*, laterally lies the *ceratobranchiad 3 part*. The rostral end of the shank bears the finger-shaped *rostral tip*. Ventral to this tip the blunt rostrad protruding *shank process* is found. The blade bears, on its rostral-medial corner, a frequently rostrad directed process: the *nipple process*. The form of the nipple process demonstrates intraspecific variability. The ventral part of the shank in particular is perforated with numerous foramina of variable diameter.

Glossohyal (Fig. 33B).

The glossohyal is a club-shaped element of which the plane of symmetry defines the relative sagittal plane. The thick end of the club lies rostrally and forms the rostrad facing *linguad hemisphere* (Fig. 7). In cross-section, the dorsal part of this thick rostral end is flat whereas the ventral side is rounded. The caudal end bears the *hyad facets* which face ventrad-laterad and caudo-dorsad. Between these facets the ventral margin forms the rostrad-caudad running, ventrad protruding *ridge* whose length varies intraspecifically.

Rostral to the hyad facets the ventral margin is dorsad incurved in a lateral view. The caudal end of the element points somewhat ventrad.

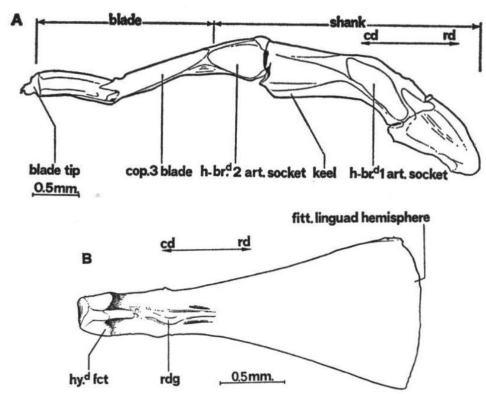


Fig. 33. A: central axis. Lateral view. The curvature in the middle part of the element is an artifact. B: glossohyal, ventral view.

Central axis (Figs 7 & 33A).

The long axis of this slender element defines its relative rostrad-caudad directions. The flat side faces dorsad. In a dorsal view the central axis is reminiscent of a spear with a short and rather thick *shank* which bears ventrally the sagittal and interrupted *keel.* The spearhead is referred to as *copula 3 blade.* and points caudad. Its caudal sharp point forms the rod-shaped *blade tip.* Just rostral to the copula 3 blade the dorsal margin is mediad incurved. This incurvation is the dorsal opening of the *hypobranchiad 2 articulation socket.* The socket is an ovoid impression in the lateral side, and its long axis runs mainly horizontal. The *hypobranchiad 1 articulation socket* is found in the caudal part of the rostral third of the lateral side. Its shape resembles that of the hypobranchiad 2 articulation socket, but it is more elongate and its long axis is rostrad-ventrad directed. In the region of the hypobranchiad 1 articulation socket the central axis bends abruptly ventrad-rostrad. The rostral end of the central axis tapers, the lateral side is incurved in cross-section.

Central cartilage (Fig. 7).

In its broadest view the central cartilage resembles a kite with a rostrad directed top. The convex face is the ventral side. The flat dorsal face defines the relative horizontal plane. The rostrad-laterad facing short sides are referred to as *hypobranchiad 3 articulation facets.* The caudal main parts of the long caudad-laterad faces are the *ceratobranchiad 4 facets,* while the small rostral parts of these faces bear the *ceratobranchiad 3 facets.*

Lower pharyngeal element (Fig. 34).

Seen on its conspicuous tooth-bearing side, this largest element in the branchial apparatus is typically heart-shaped. The dentigerous area defines the relative dorsal and horizontal face; the plane of symmetry is the relative sagittal plane. The point of the heart lies rostrally. In a dorsal view, the lateral sides are slightly incurved and the caudal side resembles a brace-type bracket.

The shape of the teeth is discussed on pp. 229–231.

Lateral-caudally the element terminates on each side in a laterad-caudad, laterad-dorsad directed process: the *horn.* The horn terminates in a laterad-dorsad facing oval with an incurved long axis: the *horn-facet.* The medial part of this facet is formed by a dorsad continuation of the medial wall of the horn: the *horn-crest.* Just ventral to the horn-crest on the lateral side of the horn an inconspicuous tip was regularly observed: the *horn-tip* (Fig. 7).

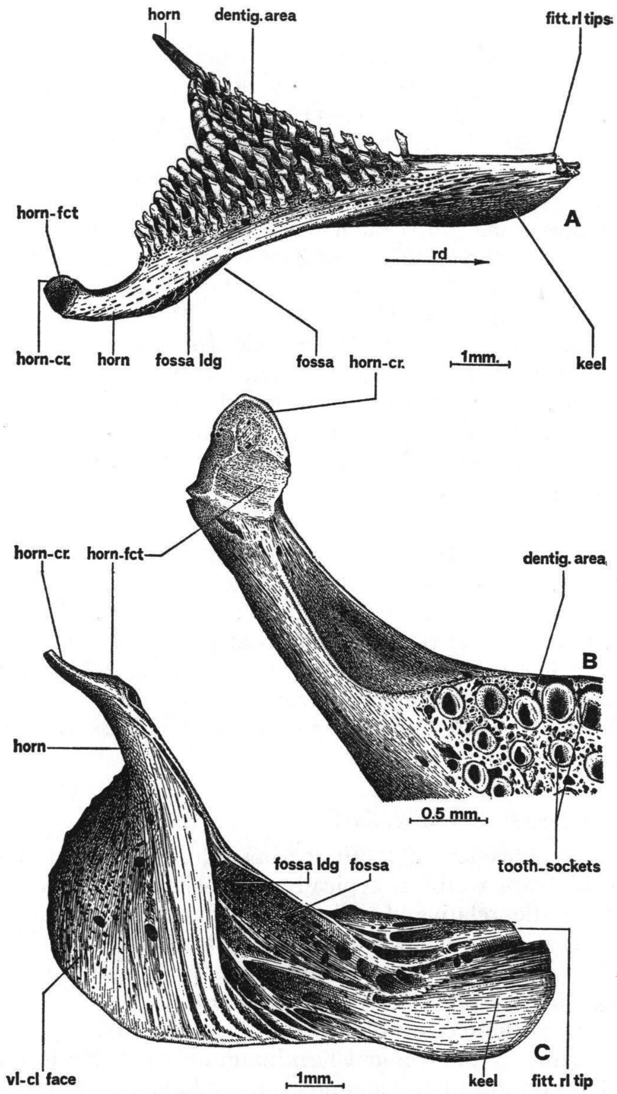


Fig. 34. Lower pharyngeal element. A: dorsal-lateral view. B: right horn. Dorsal view. C: right half. Caudal-ventral, lateral-ventral view.

The *dentigerous area* occupies almost the entire dorsal surface except for the horns and a short rostral zone.

Sagittally the rostral half of the element is provided ventrally with the sharp *keel*. Rostrally the external margin of this keel gradually curves rostrad-dorsad, only the caudal third being horizontal. The rostral origin of the keel is just ventral to the two symmetrical, rostrad directed finger-shaped *rostral tips* at the rostral-dorsal end of the element. Caudal-dorsal and caudal to the keel, the lateral walls of the lower pharyngeal element diverge laterad-caudad and become incurved in transverse section to form the *fossa*. The ceiling of the fossa is especially well-developed and formed by the laterad *fossa ledge* which is part of the lateral margin of the dentigerous area. The ventral and dorsal border of the fossa converge caudad and meet on the lateral side of the horn.

The *ventral-caudal face* is included between the ventral margins of the left and right fossa and the brace-shaped caudal-dorsal border. It consists of two symmetrical, bullate surfaces sagitally separated by a suture.

Teeth (Plates IV & V; Fig. 35)

Nomenclature on tooth-shapes (Pl. VA)

A great variety in shape is found in the teeth of *Haplochromis* species. Detailed descriptions of the jaw teeth are given by GREENWOOD in his papers on Lake George and Lake Victoria *Haplochromis* and are summarized in GREENWOOD, 1974. A major part of our terminology on tooth-shape is based on GREENWOOD's nomenclature, although the definitions are adapted to the morphological system used in this paper.

In cross-section the outline of the teeth of *Haplochromis* vary from almost round at their insertion-end to more compressed ovate distally. The general shape of the teeth may be described as cylindroids terminating distally into one to three tapering cusps. With the other end the tooth is attached to its *tooth-socket* on the pharyngeal (Fig. 34B) or jaw element. Depending on the number of cusps the teeth are referred to as *unicuspid*, *bicuspid* or *tricuspid*.

The following description applies to *H. elegans*. For bicuspid teeth the outline in cross-section of the non-cuspidate part gradually changes from (nearly) circular at the insertion-end to compressed oval at the cuspidate end. For all teeth the line through the centers of the cross-sections is the *longitudinal axis* of the tooth. The plane through the straight part of the longitudinal axis demonstrating the broadest view of the tooth, is the relative sagittal plane. Distad is the direction of the axis to the cusps, proximad the direction to the insertion end. In bi- and tricuspid teeth three zones are distinguished: insertion ring, crown and neck.

The *insertion-ring* is a ridge-like circumferential protuberance at the proximal end of all teeth. The plane through this ring is the relative horizontal plane. No discrete morphological feature marks the transition from the *neck* to the *crown*. In a view perpendicular to the sagittal plane of the tooth the outline of the crown, at least at one side, is excurved, whereas the neck-outline is incurved or straight.

Implantation may be procumbent, perpendicular or reclining. In a *procumbent* implantation the direction of the neck-part of the longitudinal axis has a definite component directing towards the nearest part of the external outline of the premaxilla in ventral view or of the mandible in dorsal view. In a *reclining* implantation this component directs away from this nearest part of the external outline.

Bicuspid teeth normally have one cusp (the *major cusp*) noticeable larger than the other (the *minor cusp*). The space included between two adjacent cusps is referred to as the *cusp-gap*.

Jaw teeth (Plates IV & VB; Figs 21A & C, 23C)

Tooth-series defined. Two sectors of teeth can be distinguished in the dentigerous areas of both premaxilla and mandible. The *outer series* consisting of mainly bicuspid, relatively stout teeth and the *inner series* of several irregular rows of relatively small, compressed, mainly tricuspid teeth.

Outer series (Pl. IV, VB): Teeth are slightly curved. The curvature curves distally away from the sagittal plane of the tooth, and has an internad component with regard to the element on which the tooth is implanted. Cross-sections of the neck are nearly circular in outline, whereas the cross-section outline of the crown is oval. The implantation is perpendicular, except for the slightly procumbent teeth in the rostral half of the mandibular outer series (GREENWOOD, 1973). The majority of unworn teeth in wild adult specimens are unequally bicuspid. With the sagittal plane of the tooth oriented parallel to the sagittal plane of the jaw, the major cusp is, with rare exception, rostrally in position. The peculiar shape of the inner face of the major cusp is best given by quoting the description of GREENWOOD (1973): "Some teeth in each jaw have one margin of the major cusp partly flattened from below the tip so that it appears as a narrow step-like *flange* adjacent to the minor cusp ...". In a counting from unworn teeth of wild, adult specimens 32 out of 56 teeth were provided with such a step-like flange. Besides bicuspid teeth, caudally some unicuspid or tricuspid teeth may be found. Rostral-caudad the vertical tooth-length decreases from 1 mm to 0.3 mm. GREENWOOD (1973) counted 34–42 (mean 38) teeth for the total outer series of the upper jaw. Our

figures are in the same range. In the mandible (half the lower jaw) 14–17 teeth (mean 15) were found.

Special attention should be paid to the aberrant teeth of the so-called "overgrown" specimens (see fig. 2). *H. elegans* of $\pm$ 100 mm has slightly curved ,unicuspid teeth (Fig. 23C). We gained the impression that change from bicuspid to unicuspid teeth took place at a length of $\pm$ 95 mm. The unicuspid character was not caused by abrasion, because erupting teeth and teeth still in the alveolar space are already unicuspid. The changes occurred in overgrown specimens which were originally caught in Lake George and which reached this unnatural length in our tanks. Entirely unicuspid teeth were also observed for similar overgrown *H. nigripinnis* and *H. angustifrons* which also possess bicuspid teeth at a natural adult length. Although adult wild *H. squamipinnis* have unicuspid teeth, young fishes up to at least 78 mm do have mainly bicuspid teeth. Unicuspidity of all mandibular teeth, except one, was observed only at a length of 97 mm (JOSEMANS & VAN DE VELDE, pers. comm.), a figure which agrees well with the 95 mm as the length of change for *H. elegans*.

Inner series (Fig. 21C): Irregular rows of relatively small, compressed, mainly tricuspid teeth make up the inner teeth series. Two or three rows of teeth occupy the mediad curving part of the dentigerous area; in the caudo-lateral part only the outer row is continued, but it does not reach as far caudal as the outer series. The premaxillary teeth of the inner row(s) are reclined, the outer row of the premaxillary and all mandibular teeth are more or less perpendicularly implanted. Besides the majority of tricuspid teeth, a very few unequally bicuspid teeth were observed. Counts for three premaxillae gave 39, 32 and 31 as the number of teeth in the inner series. Similar counts for three mandibles gave 36, 29, 35 teeth.

Pharyngeal teeth (Plate VA; Figs 34A & 35)

The shapes of the pharyngeal teeth (Pl. VA; Fig. 34). The shapes of the crowns of the pharyngeal teeth may be described as variations on four themes: the number of cusps, the position and curvature of the major cusp, and the degree of excurvation of the outline near the minor cusp.

Cuspidation varies from unicuspid to tricuspid. The tricuspid teeth on the pharyngeal elements differ from tricuspid jaw teeth in the following facts:
(1) the external position of the major cusp in pharyngeal teeth. The major cusp is centrally situated in jaw teeth; (2) the incurved outline of the cusp-gaps in pharyngeal teeth. This outline is a reentrant angle

in jaw teeth; (3) the two smaller cusps are unequal in pharyngeal teeth and equal in jaw teeth. Even in well-developed tricuspid pharyngeal teeth the smallest cusp (the *cusp-protuberance*) is only an inconspicuous protuberance proximal to the middle *minor cusp*. The cusp-gap between minor cusp and cusp-protuberance (the *minor cusp-gap*) is a shallow incurvation. The incurved outline of the cusp-gap between major and minor cusp (the *major cusp-gap*) varies in degree of curvature from nearly straight in the lower pharyngeal teeth (bevelled kind, see below) to semicircular in the upper-pharyngeal teeth with well-developed major and minor cusps (hooked kind, see below). The degree of curvature of the major cusp varies from a hook-like axiad-curved cusp to an externad-distad directing cusp. When the major cusp is situated outside the neck cylinder, the cusp is *reclining*. In sagittal view the crown-margin proximal to the minor cusp or cusp-protuberance, varies from slightly excurved to a pronounced excurvation. In cross-section the non-cuspidate part of the crown of a pharyngeal tooth is oblong with its long axis running sagittally. The sharper point of this oblong shape lies at the minor cusp side of the tooth. The cross-section of the neck seems to be more symmetrically oval. Three kinds of pharyngeal teeth will be distinguished: hooked, bevelled and pronounced. The *hooked kind* is a bi- or tricuspid tooth with an axiad-curved, hook-like major cusp and well-developed major and minor cusps. The incurvation of the major cusp-gap is semicircular. The *bevelled kind* has a distad directed major cusp. The minor cusp is absent or little developed and the major cusp-gap is

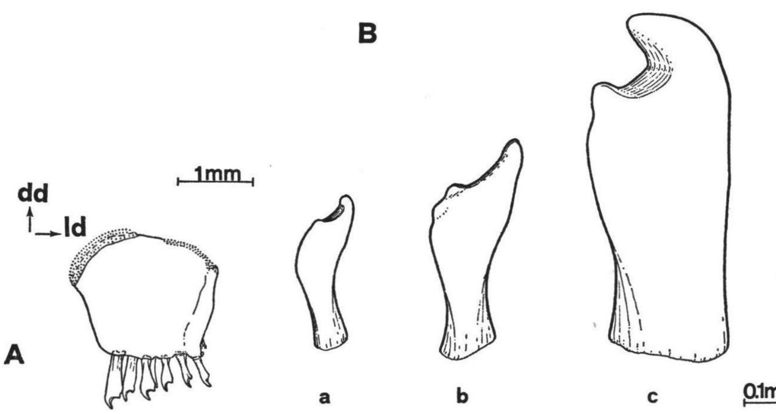


Fig. 35. A: right pharyngobranchial 2 with teeth. Caudal view. B: pharyngeal tooth-kinds. View on sagittal plane of the teeth. a: pronounced, b: bevelled, c: hooked.

nearly straight or shallowly incurved. The *pronounced kind* has a reclining major cusp and a pronounced excurved crown margin near the minor cusp or cusp-protuberance.

Teeth of pharyngobranchial 2 (Fig. 35A). From 5 to 7 well-developed, perpendicularly implanted teeth are found on pharyngobranchial 2 of adult wild specimens. With regard to pharyngobranchial 2, tooth-length decreases from medial to lateral. The teeth are of the hooked kind, the major cusp-gap faces laterad-ventrad with regard to the reference-grid of pharyngobranchial 2. In pharyngobranchial 2 the sagittal planes of the teeth are perpendicular to the sagittal plane of pharyngobranchial 2. The sagittal planes of the teeth on the lower pharyngeal element and on pharyngobranchial 3,4 coincide with parasagittal planes of these elements.

Teeth of pharyngobranchial 3,4 (Pl. VA). Among the teeth of pharyngobranchial 3,4 the three kinds (see above) and intergrades may be distinguished, although bevelled kinds seem to be rare. The teeth are perpendicularly implanted and parallelly oriented. The major cusp-gap faces ventrad-caudad with regard to the directions of pharyngobranchial 3,4. Teeth in the rostral-medial corner of the dentigerous area are stout and of the hooked kind. Especially in the caudo-lateral dentigerous zone, the minute teeth are of the pronounced kind. Vertical tooth-lengths decrease in a rostral-caudad order and in a medial-laterad order with regard to the directions defined for pharyngobranchial 3,4. For three pharyngobranchials 89, 91 and 87 teeth were counted.

Teeth of the lower pharyngeal element (Fig. 34A). As in pharyngobranchial 3,4, teeth are parallel, and are perpendicularly implanted. In contrast to pharyngobranchial 3,4, the major cusp-gap in the lower pharyngeal teeth faces rostrad-dorsad with regard to the direction defined for the lower pharyngeal element. The majority of the teeth on the lower pharyngeal element are of the bevelled kind. Only in the caudal transverse series slightly hooked teeth are found. Counts for *halfs* of *three* lower pharyngeal elements gave *total* teeth numbers of 2 × 88; 2 × 66; 2 × 91. In contrast to those on pharyngobranchial 3,4 the rostral teeth on the lower pharyngeal element are the smallest ones and the caudal the stoutest.

Hyoid and branchiostegal apparatuses (Figs 5, 36–39)

Hyoid (Fig. 36)

In broadest view the hyoid resembles a carving knife. The handle

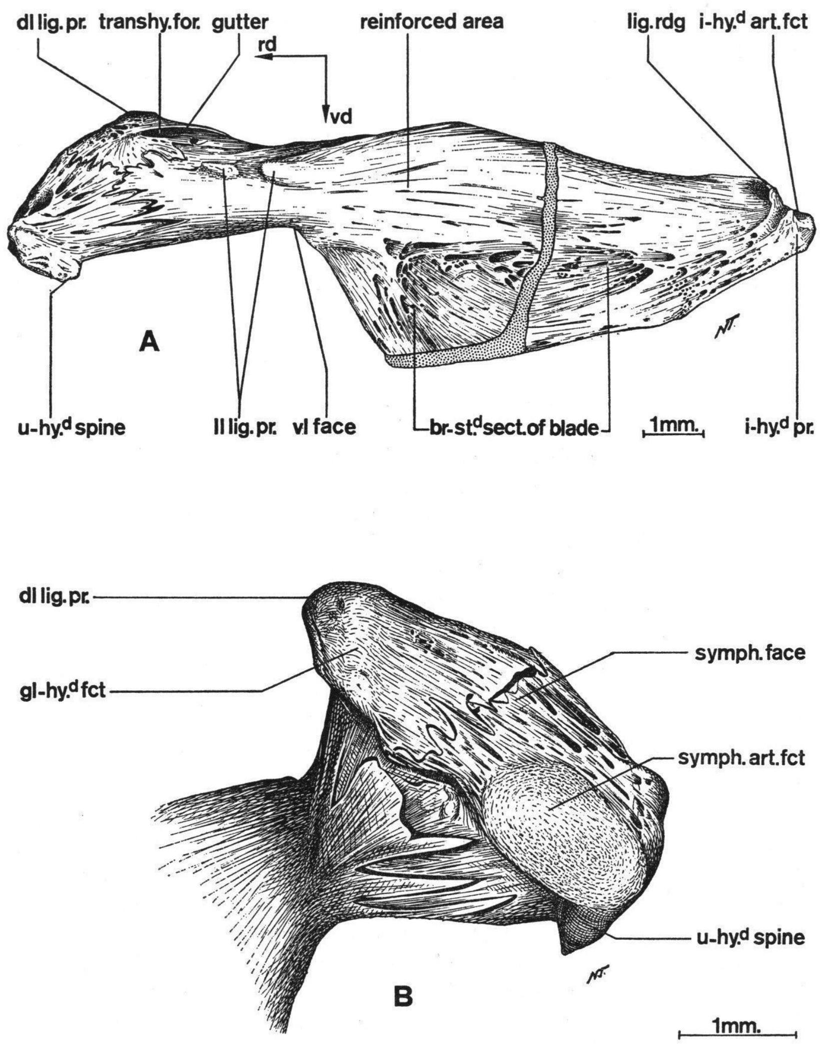


Fig. 36. Left hyoid. A: lateral view. B: symphyseal face. Rostro-medial view.

of the knife is referred to as the *handle* and the blade-like part as the *blade region*. The plane through the blade region is the relative sagittal plane. The line through the two terminal and most remote points of the element in broadest view, defines the relative horizontal, the handle lying rostrally.

For its greater part the outline of the blade region in cross-section can be described as oddly P-shaped. Caudad the P-outline is gradually lost. The ventrad directed stick of the P is the *blade,* whereas the laterad excurved part will be referred to as the *reinforced area.* The *branchiostegad* sector is a scalloped part in the lateral face of the blade. In lateral view the outline of the branchiostegad sector is triangular.

Caudal to the blade the hyoid is continued as the *interhyad process* which bears, on its dorsal surface, the *interhyad articulation facet.* Dorso-rostral to this facet a laterad-rostrad facing concavity is found in the lateral wall. Dorsally this concavity is medially and caudally bordered by a ridge: the *ligament ridge.* The ridge is hook-shaped in dorsal view, the curved part lying caudally.

In the handle the dorsal border of the hyoid deviates mediad and dorsad from its caudad course in the blade region. Whereas the ventral third of the handle lies sagittally, the dorsal part appears as a mediad twisted, latero-dorsad facing triangle. The dorsal vertex of this triangle is elevated into the *dorsal ligament process.* In this triangular zone the conspicuous *transhyoid foramen* is found. The floor of this foramen is continued caudad as a latero-dorsad facing gutter-like depression on the lateral side of the handle (the *gutter*). It reaches the dorsal border of the hyoid at the rostral origin of the blade region. The rostral-ventral corner of the handle contains the ventrad-caudad directed *urohyad spine.* The medio-rostrad facing rostral margin of the handle between the urohyad-spine and dorsal ligament process is the *symphyseal face,* of which the long axis runs dorsad-caudad, medio-dorsad. The symphyseal face bears dorsally, on the dorsal ligament process the *glossohyad facet* and ventrally the oval *symphyseal articulation facet.* The remaining two processes to be distinguished on the handle are the *lateral ligament processes*: two blunt protuberances on the lateral face, pointing towards each other. In its caudal third the ventral border of the handle broadens somewhat to form the *ventral face* which bears caudally a ventrad facing concavity: the *branchiostegad recess.*

Branchiostegal rays 1–5. (Figs 5, 37 & 38)

The five branchiostegal rays resemble each other in being slender, curved, spinous elements. They are numbered 1–5 in a rostral-caudad order. The line connecting both ends runs, by definition, rostrad-caudad, the pointed end lying caudally. The longitudinal axis of the ray is curved ventrad. The zone near the rostral end is referred to as the *articulation zone.* Excepting ray 1, the articulation zone of each ray bears, medially, on the dorsal margin, an ovoid mediad facing articulation patch: the *hyad articulation patch.* The position of this patch is best detected from serial sections. Terminally the articulation zone bears a

mediad protuberance: the *ligament protuberance*. The *rostral flange* is a dorsad extension from the medial side of the body of rays 2–5 in their rostral parts. The flange-character is not very clear and it is best observed from a cross-section. The dorsal part of the hyad articulation patch is medially attached to the rostral part of the flange (the *articulation part* of the rostral flange). The *ventral ridgelet* on rays 2, 3 and 4 is found as part of the ventral margin on the caudal part of the rostral third of the element. Its shape is best understood from cross-sections, where the ridgelet appears as the tail of the oddly comma-shaped outline. The tail points mediad-ventrad or medio-ventrad. The rostral and caudal end of the ridgelet are arbitrarily defined; it disappears gradually in the general surface of the element. Following rostral-caudad cross-sections through the branchiostegal rays the general outline of rays 2–5 gradually flattens mediad-laterad, whereas the oval outline of ray one is retained nearer to a circular aspect.

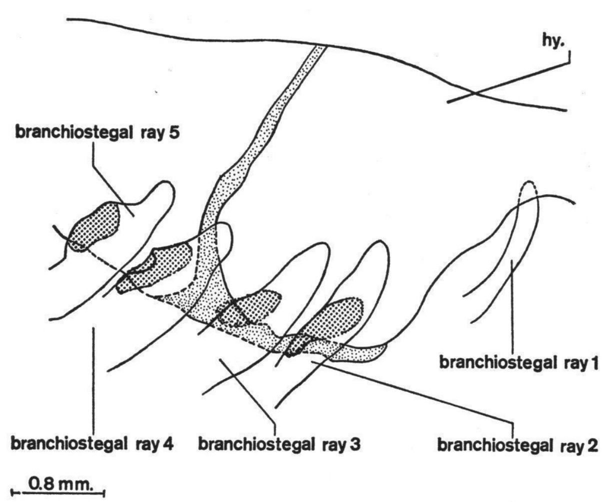


Fig. 37. Branchiostegal apparatus. Absolute lateral view. The dotted areas on the medial face of the branchiostegal rays are the hyad articulation patches.

Differences between the rays are small and chiefly concern the size, hyad patches, rostral flange and ridgelet. As mentioned before, no ridgelet is found in rays 1 and 5. In a rostral-caudad order the elements increase in size and the articulation part of the rostral flange becomes more and more apparent. Intraspecific variation is great, however. Generally speaking the articulation part of the rostral flange

of 5 is relatively well-developed; this articulation part often seems to be absent in 2 and sometimes in 3. The articulation part of the rostral flange of 4 sometimes bears a spinous process. The outline of the articulation patches varies, but it seems that the outline of 2 is a characteristically elongate oval as compared to the more rounded ovals of 3–5.

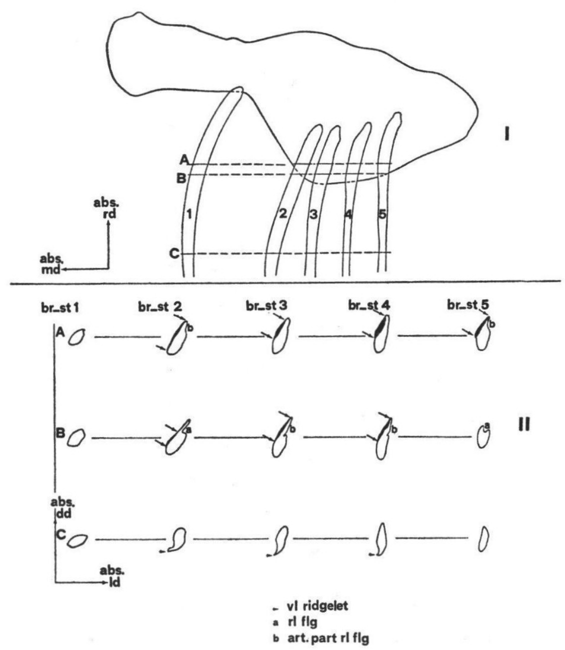


Fig. 38. Right branchiostegal apparatus. I: absolute ventral view of the branchiostegal apparatus in an expanded head. II: outline of absolute transverse sections through the rays at the levels indicated in A. The thick black margins between the arrows indicate the hyad articulation patch.

Interhyal (Fig. 39)

The interhyal is a rod-shaped element in which the longitudinal axis defines the vertical direction. Halfway along its vertical length the element is mediad-laterad flattened. In cross-section one of the sides appears to be incurved over half the vertical length of the element (the *ligament depression*). This depression tapers dorsad and marks the ventral half of the rostral side. Medially the depression is protected by the rostrad protruding vertical *ridge*. The interhyal terminates

dorsally in the *suspensoriad articulation facet*, ventrally in the *hyad articulation facet*. In a rostral view the lateral side forms ventrally a bullate laterad swelling.

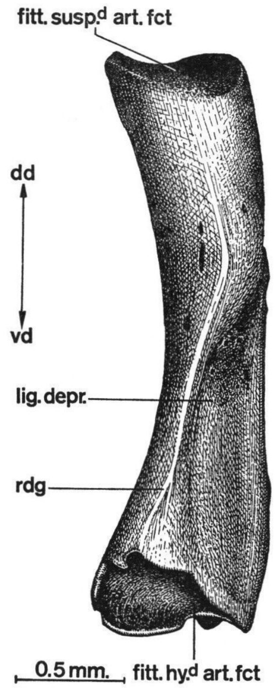


Fig. 39. Left interhyal. Rostro-medial view.

Urohyal (Fig. 40)

Seen on its flat side, the outline of the urohyal can be described as a triangle provided with a spine on one of its sides near the acute vertex. The plane of the triangle is the relative sagittal plane. For its greater part the urohyal consists of a thin, triangular *lamella*. The relative horizontal side of the lamella bears the laterad-ventrad directed ventral *wing* on each side. The left and right wing surround the *wing fossa*. The caudal margin of the urohyal is the caudo-dorsad running and undulating caudal border of the lamella. The dorso-caudad running dorsal side of the lamellar triangle is reinforced by the laterad protruding *dorsal ridge*. Except for a short rostral and caudal section, left and right dorsal ridges include the dorsad facing *ridge groove*. The

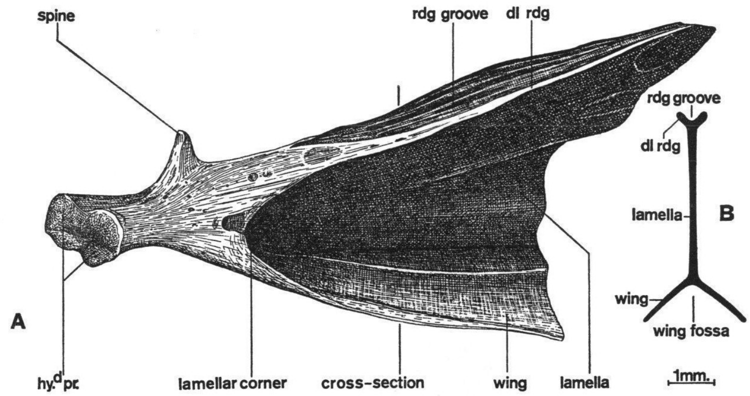


Fig. 40. Urohyal. A: rostro-lateral, dorso-lateral view. B: cross-section.

dorsal ridge and the ventral wings meet at the *lamellar corner* .Rostral to the lamellar corner three processes are located. On each side the short, stout, *hyad process* protrudes latero-rostrad and somewhat ventrad. The *spine* is a dorsad process on the dorsal margin near the rostral vertex of the urohyal. The shape of the spine varies intraspecifically.

Shoulder girdle apparatus (Figs 41, 42 & 43)

Pectoral element (Fig. 41)

The pectoral element can be described as an elongate body provided with two flanges. The body of the element is curved and terminates at each end in a spinous process. The line connecting the tips of these processes defines the relative dorsad-ventrad directions. The longitudinal axis of the body of the element is curved caudad. Of the two flanges, the *coracoid flange* is perforated by two foramina. The non-perforated flange is called the *lamella.* The lamella is attached to the lateral margin of the dorsal part of the body of the perctoral element and faces, by definition, laterad. In the rostral-dorsal corner of the lamella the *supracleithrad impression* is found, marked by a ventrad curved ridgelet.

The *rostral face* is the elongate caudad incurved side of the pectoral element. The rostral face can be divided into three parts: (1) the *dorsal zone* which faces mainly ventro-rostrad, (2) the *ventral zone* which faces mainly dorso-rostrad and, medially attached to the ventral zone, (3) the *parasagittal ledge*, an elongate crest of variable depth with a rostrad-laterad facing vector.

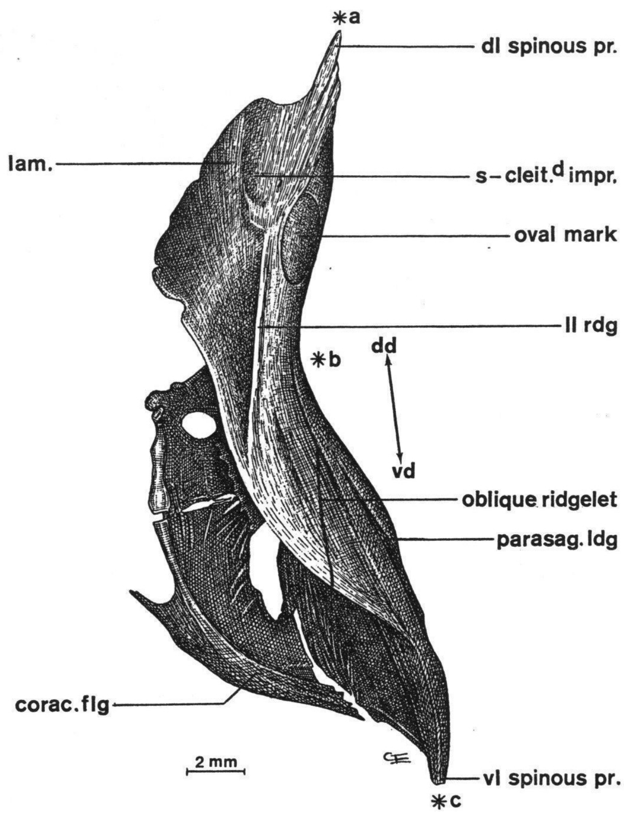


Fig. 41. Right pectoral element. Rostral-lateral view. Between a–b the dorsal zone of the rostral face is comprised, between b–c the ventral zone.

On the ventral zone the inconspicuous medio-dorsad running *oblique ridgelet* is found. The ventral zone terminates in the *ventral spinous process.*

The lamella is thin and laterally attached mainly to the dorsal zone. The transition from dorsal zone to the lamella is sharp and for the greater, ventral part it is marked by the caudo-ventrad running *lateral ridge.* The dorsal zone is narrow as compared with the ventral zone and tapers dorsal to the *dorsal spinous process.* Ventral to the dorsal spinous process it bears the *oval mark* of which the surface is coarse as compared with the remaining surface.

As the *coracoid flange* is mainly related to the pectoral fins, its shape will not be discussed.

Supracleithrum (Fig. 42)

In broadest view the outline of the supracleithrum is approximately triangular with curved sides. The plane through the vertices is the relative sagittal plane. The feebly excurved and longest side is the rostral one. The caudal vertex is situated at about one third of the vertical depth and nearer to the ventral vertex. The shape of the margins connecting the caudal vertex with the dorsal and ventral vertices demonstrates intraspecific variation: *e.g.* the curvation of the ventral-caudal margin varies in depth.

The zone of the dorsal vertex is, on a lateral view, marked by two facets between which the *dorsal foramen* opens laterad-dorsad. The uppermost facet is the *dorsal posttemporad facet.* It faces dorso-laterad. The outline of the *ventral posttemporad facet* is oval and better demarcated than that of the dorsal posttemporad facet. The dorsal posttemporad facet faces latero-dorsad.

On the margin between the ventral posttemporad facet and the caudal vertex the *caudal foramen* opens caudad-ventrad. In most pre-

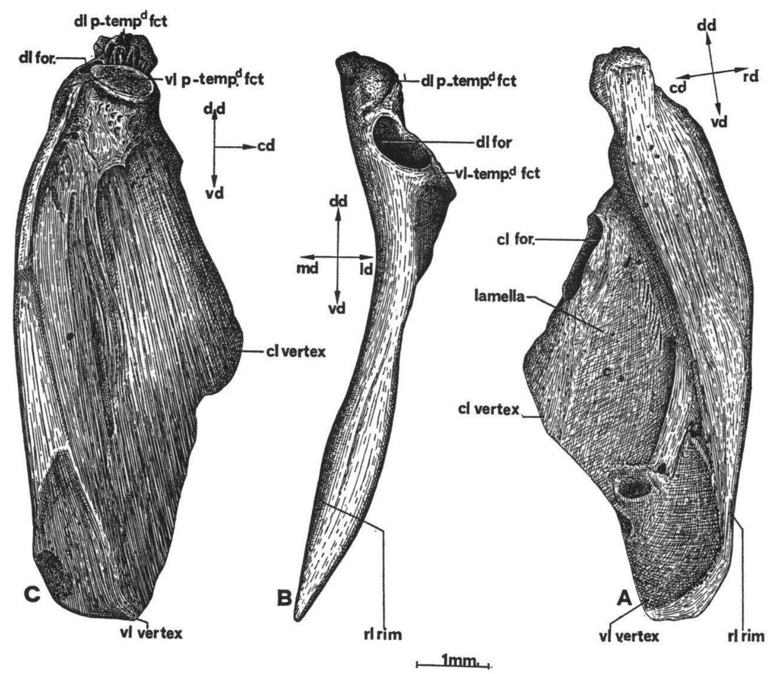


Fig. 42. Left supracleithrum. A: medial view. B: rostral view. C: lateral view.

parations the opening is only to be seen from a medial view, its lateral aspect being a notch in the dorsal-caudal margin.

A medial view on the supracleithrum shows the excurved rostral margin to be reinforced with the well-developed mediad elevated *rostral rim*. The remaining part is the thin caudad extending triangular *lamella*. The rostral part of the caudal-dorsal side of the lamella bears the caudal foramen and part of the canal which connects the two foramina. The rostral part of this canal disappears in the reinforced rostral rim.

Posttemporal (Fig. 43)

The posttemporal is a Y-shaped element with unequal arms and the short, thick *handle*. Although when in situ the plane through both arms faces rostrad-laterad, it is, for descriptional convenience, defined as the relative transverse plane of the posttemporal. The *dorsal arm* is the larger one and marked by its flattened termination (the *nail*). The direction towards the nail of the long axis of the dorsal arm marks the mediad direction. The caudal face is found as that side of the handle where the junction zone of both arms merges into the *apophysis* bearing the laterad-ventrad facing ovoid *dorsal supracleithrad facet*. The ventral aspect of the handle is provided laterally with the caudo-ventrad facing *ventral supracleithrad facet*. Between this facet and the insertion of the ventral arm the *medial-ventral foramen* opens mainly latero-ventrad. A rostral view reveals the remaining two lateral line foramina. In the lateral third of the handle the *lateral foramen* opens latero-rostrad. The size of the opening as well as the shapes of the surrounding parts demonstrate conspicuous intraspecific variability. Near the reentrant angle formed by both arms the *medial-rostral foramen* opens medio-rostrad. The *ventral arm* is stick-like and about half as long as the dorsal one. The arms are nearly perpendicular to each other.

Primary lateral line elements (Figs 4, 8, 44 & 45)

Nasal element (Fig. 44)

An elongate tube and a lamella attached along one of its long sides are the two main components of the nasal element. The two parts are referred to as the *canal region* and the *lateral flange*. The plane through the lateral flange is the relative horizontal plane. The long axis through the straight margin of the canal region defines the rostrad-caudad directions. At both ends the canal opens through a conspicuous (lateral line) foramen. The larger of the two is the *caudal foramen* and the smaller the *rostral foramen*.

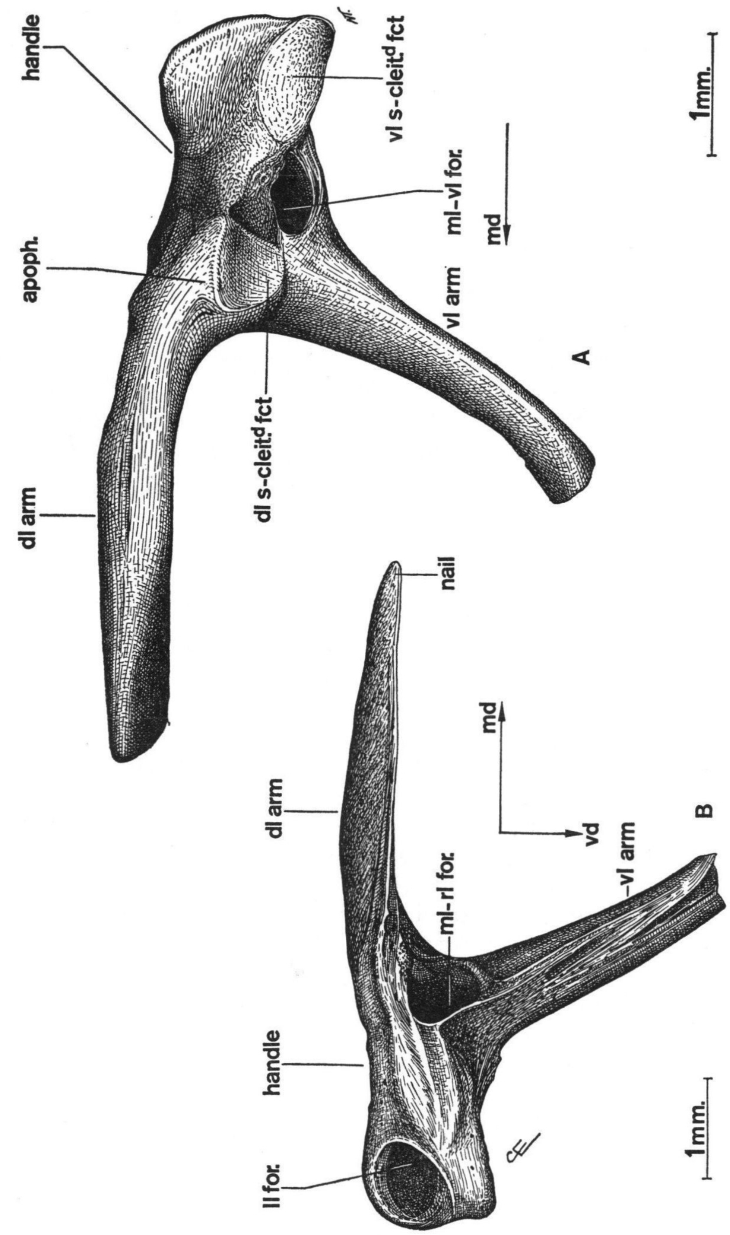


Fig. 43. Right posttemporal. A: ventro-rostral view. B: caudal view.

The deep mediad *incurvation* interrupts the lateral flange in its rostral half. The small *medial flange* is found attached to the rostral medial corner of the canal region.

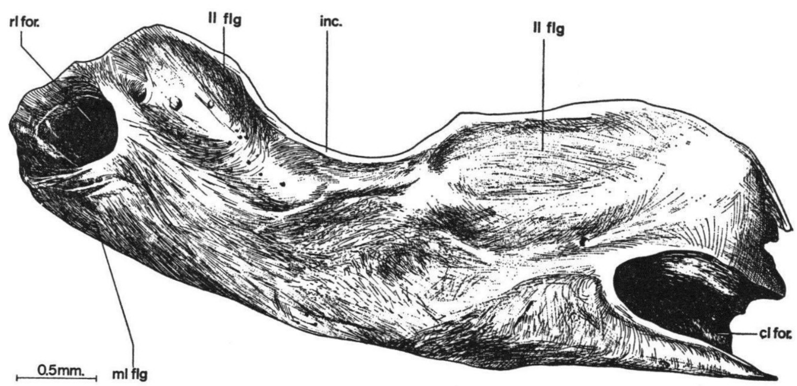


Fig. 44. Right nasal. Dorsal view.

Infraorbital apparatus, including the lacrimal (Figs 8 & 45)

Except for the dorsal part, the eye is surrounded by a series of canal-bearing bones: the infraorbitals. The rostral and most extensive one is called the *lacrimal.*

The lacrimal is a flat, roughly trapezoid-shaped element with a conspicuous process extending from the rostro-dorsal corner (the *ear*). The hollow side of this ear faces caudad. The plane through the element defines the relative sagittal plane. On its lateral face five lateral line foramina open in different directions. The line through the margin of the lacrimal, onto which three of these foramina open, makes up the rostrad-caudad directions. The first lacrimal lateral line foramen (*LLF_1*) opens rostrad from the base of the ear. In contrast to the four remaining foramina, LLF_1 opens near the margin and has a circular outline. LLF_{2-5} are semicircular and they are situated at some distance from the border. LLF_{2-4} all face mainly ventrad. *LLF_2* is ventrad directed to the rostral third of the ventral margin. *LLF_3* faces ventrad and a little caudad to the middle third of the ventral border. The caudo-ventrad directed *LLF_4* opens onto the ventral-caudal corner of the lacrimal. *LLF_5* is found as a caudad facing opening at the dorsal-caudal corner. In a different way LLF_{2-5} may be described as the peripheral openings of a series of canaliculi of different lengths converging to an area caudal to LLF_1.

The medial view of the lacrimal reveals a conspicuous vertical pillar-shaped process at the caudal-medial corner of the ear: the *neurocraniad pillar*. Dorsally it bears the flat rostro-dorsad directed *neurocraniad articulation facet*. Ventral to the pillar the extensive *dent* is found on the medial surface.

The caudal half of the dorsal margin is broadened and is referred to as the *caudo-dorsal broadening*.

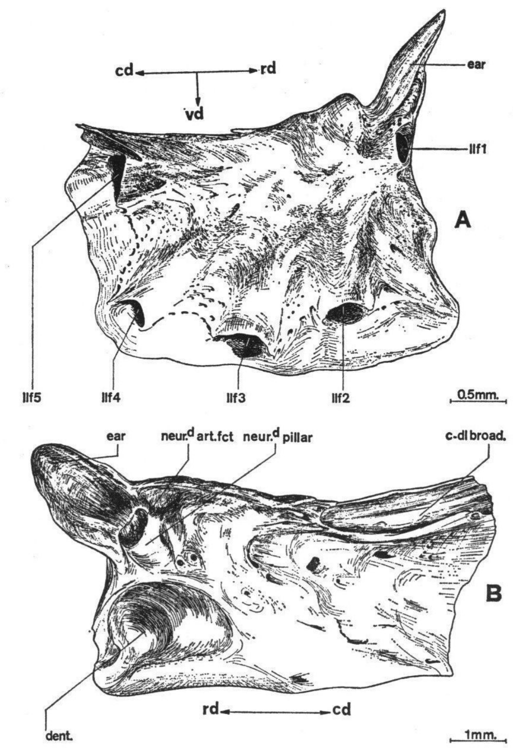


Fig. 45. Right lacrimal. A: lateral view. B: dorso-medial view.

Extrascapulae (Fig. 4)

Two tube-shaped elements are found in the skin dorsal to the lateral point of the supratemporal. The medial-dorsal one of these two elements is the *medial extrascapula* (the lateral extrascapular, BRANSON, 1961); it is a short tube. The *lateral extrascapula* (the supratemporal intertemporal, BRANSON, 1961) is chevron-shaped, bearing a foramen at each vertex.

EXAMPLES OF TROPHICALLY CORRELATED SHAPE DIFFERENCES IN SOME OTHER HAPLOCHROMIS SPECIES

Introduction

As has been stated in the section on methods, trophically correlated shape differences were observed during our cursory observations of skeletal material of various *Haplochromis* species from Lake George and Lake Victoria. Two examples of such differences will be given in the following sections. One concerns paedophagous species and their characteristic shape-features in the palatine region of the suspensorium. The other example describes the typical shape of pharyngobranchial 3,4 in intrapharyngeal mollusc-crushing species. The main reasons for including these examples in the present paper are two fold:

1. These examples illustrate the applicability to comparative functional morphology of the technique for describing shapes which was developed in the present paper.
2. The examples demonstrate the usefulness of a strict comparative technique for tracing in *Haplochromis* species those shape differences which are *correlated* with functions, without knowing, for the moment, what kind of relationship there is between these shapes and the functions.

The intrapharyngeal mollusc-crushing *Haplochromis* species crack snails (or shells) between pharyngobranchial 3,4 and the lower pharyngeal element. Selection of these elements for comparative investigations of their shapes is therefore strictly guided by the anticipated information on their function. The overall qualitative impression of their stoutness as compared to pharyngeal elements in insectivorous species was already noted in the various papers of GREENWOOD, 1960 on molluscivorous *Haplochromis* species. The detailed description of the shape of pharyngobranchial 3,4 is mainly included to indicate the effectiveness of the present nomenclatorial system for describing and screening functionally relevant differences in *Haplochromis* species and for quantifying such differences. Some *Haplochromis* species from Lake Victoria are ambivalent in their food-preferences. *H. obtusidens* is an insectivorous as well as an intrapharyngeal mollusc-crushing species. Related to the combination of these two functions, this species indeed demonstrates both insectivorous and molluscivorous features in the shape of its pharyngobranchial 3,4. The degree to which either of the features dominates in the various shape aspects of pharyngobranchial 3,4 can be expressed quantitatively, using the shape description of pharyngobranchial 3,4 of *H. elegans*.

Morphological comparison between various trophic types of *Haplochromis* species from Lake George showed a number of shape differences

correlated with the varieties of food. Further arguments in favour of a *functional* significance of these differences were found in *Haplochromis* species from Lake Victoria. Species of the same trophic types in both lakes exhibit the same shape differences. As the species flocks of both lakes evolved independently from the same ancestors, it becomes highly probable that the shape differences are indeed attributable to the differences in function. The preceding method for tracing functional relevant morphological differences is especially important when information on function is scanty. For instance: among the trophic types of *Haplochromis* species a group of so-called paedophages is described by GREENWOOD (1959). These species feed on buccal ontogenetic stages of *Haplochromis*. The food-type is known from the stomach-content of the paedophagous species but no observation on the feeding-action is available. This means that information on the function is lacking. Presupposing that one feeding mechanism underlies the paedophagous habit and that feeding is a dominant function of the muscle-skeleton-ligament system in the fish-head, the skeletal elements of the paedophagous *Haplochromis* species of Lake Victoria and Lake George were compared with *H. elegans*. Parts of the skeleton did indeed demonstrate characteristic features which, as far as information is available, only occur in paedophages. The example given below describes these "paedophagous" features of the palatine region.

Table I lists the various species studied in this section.

TABLE I

Distribution and feeding habits of the species studied in the section on trophically correlated shape differences.

Spec. nr.	*Species*	*Lake**	*Feeding habit*	*Reference*
004	*H. taurinus*	LG	paedophagous	GREENWOOD 1973
006	*H. elegans*	LG	insectivorous	DUNN 1972 GREENWOOD 1973
016	*H. mylodon*	LG	intrapharyngeal mollusc-crushing $\gg$ insectivorous	GREENWOOD 1973
025	*H. obtusidens*	LV	insectivorous & intrapharyngeal mollusc-crushing	GREENWOOD 1960
027	*H. obesus*	LV	paedophagous	GREENWOOD 1959
029	*H. maxillaris*	LV	paedophagous	GREENWOOD 1959
032	*H. parvidens*	LV	paedophagous	GREENWOOD 1959
037	*H. microdon*	LV	unknown; presumably paedophagous	GREENWOOD 1959
041	*H. pharyngomylus*	LV	intrapharyngeal mollusc-crushing	GREENWOOD 1960
043	*H. barbarae*	LV	recently fertilized ova	GREENWOOD 1967

* LG = Lake George, LV = Lake Victoria.

Pharyngobranchial 3,4 in intrapharyngeal mollusc-crushing species

Definition of measurements (Fig. 46)

The quantitative comparison of the shapes of the pharyngobrancials 3,4 is based on the following measurements:

1. *Total length of pharyngobranchial 3,4* (Fig. 46A: t). The total length is defined as the distance between the transverse planes through the most rostral and most caudal point of pharyngobranchial 3,4.

2. *Length of the pharyngobranchial 3 region* (Fig. 46A: p). The length of the pharyngobranchial 3 region is measured as the distance between the transverse planes through the rostralmost point of pharyngobranchial 3,4 and through the most caudal end of the pharyngobranchial 3 part of the caudal face.

3. *Length of the neurocraniad apophysis* (Fig. 46A: n). This is the distance between the transverse planes through the rostral margin of the epibranchiad 2 articulation facet, and through the caudalmost point of the neurocraniad articulation facet.

4. *Length of the smooth part of the neurocraniad articulation facet* (Fig. 46A: s). This length is measured as the distance between two transverse planes, through the most rostral and most caudal point of the smooth area.

5. *Squareness of outline in dorsal view* (Fig. 46B). The squareness is measured as the angles between four lines along the outline of the pharyngobranchial, seen in dorsal view. These four lines are defined as follows. The *line AC* runs rostrad-caudad along the medial face (Fig. 46B: AC). The *line AB* is drawn through the medial point of the transverse crest and the most rostral point of the caudal-lateral

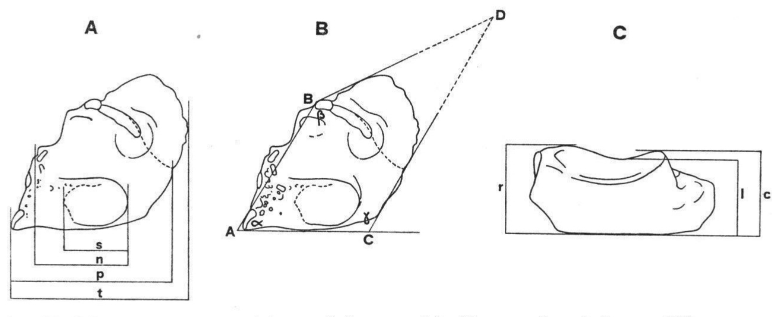


Fig. 46. Measurements used in studying trophically correlated shape-differences of pharyngobranchial 3,4 in *H. elegans* and intrapharyngeal mollusc-crushers. The measurements are defined in the text on pp. 246–247. A: length measurements. (Right pharyngobranchial 3,4 of *H. elegans*. Dorsal view). B: angle measurements. (idem). C: height measurements. (Right pharyngobranchial 3,4 of *H. mylodon*. Medial view).

eminence (Fig. 46B: AB). The line AB runs mainly along the valley border. The *line BD* connects the rostral lateral point of the caudal lateral eminence with the most lateral point of the pharyngobranchial 4 region (Fig. 46B: BD). The *line CD* is defined through the caudal end of the suture and the point where the border of the caudal face curves latero-caudad (Fig. 46B: CD).

6. *Rostral height of the neurocraniad apophysis* (Fig. 46C: r). In medial view the rostral height of the neurocraniad apophysis is the vertical depth of the highest point of the rostral end of the neurocraniad articulation facet.

7. *Caudal height of the neurocraniad apophysis* (Fig. 46C: c). In medial view the caudal height of the neurocraniad apophysis is the vertical depth of the most caudal point of the neurocraniad articulation facet.

8. *Height of the lowest point of the neurocraniad articulation facet* (Fig. 46C: l). In medial view the height of the lowest point of the neurocraniad articulation facet is the vertical depth of the most ventral point of this facet.

Shape differences (Figs 47, 48, 49; Table II)

For pharyngobranchial 3,4 the trophically correlated shape differences between *H. elegans* and intrapharyngeal mollusc-crushers may be summarized as follows:

1. *Outline in dorsal view.* (Fig. 47). In the series *H. elegans, H. obtusidens, H. mylodon, H. pharyngomylus* the outline of pharyngobranchial 3,4 in dorsal view changes from relatively ovoid to more or less square. The degree of squareness is measured as the angles between the four lines (p. 246, Fig. 46B) which comprise the outline of the elements, seen in dorsal view. In an ideally square element the angles should be 90^0. As can be gleaned from Table II the squareness increases in the species series mentioned above (Table II: α, β, γ). In the series *H. elegans, H. obtusidens, H. mylodon, H. pharyngomylus* the increasing squareness is related to the following facts:

a. *Position of the caudal-lateral eminence and of the pharyngobranchial 4 region* (Fig. 47). The position of the caudal-lateral eminence and the pharyngobranchial 4 region shifts relatively rostrad.
b. *Incurvation of the valley border.* The valley border changes from incurved to straight.

2. *Differences in the rostral-medial eminence.*

a. *Length of the neurocraniad apophysis* (Fig. 47, Table II: t, p, n, n/t, n/p). In the series *H. elegans, H. mylodon, H. pharyngomylus* the length of the neurocraniad apophysis increases with regard to the total length of pharyngobranchial 3,4 and also with regard to the

Fig. 47. Right pharyngobranchial 3,4. Dorsal view. Arrows point to the gutter-like impression discussed in the text (pp. 250, 252). Scale = 1 mm.

length of the pharyngobranchial 3 region. In one specimen of *H. obtusidens* (W-025-003) the ratio is like that of *H. elegans* and in the other specimen (W-025-001) this ratio lies between that of *H. elegans* and *H. mylodon*. The longer apophysis in *H. mylodon* and *H. pharyngomylus*, together with their more rostrally situated caudal-lateral eminence contribute to the obliteration in a medial view of the caudal-lateral eminence (Fig. 48).

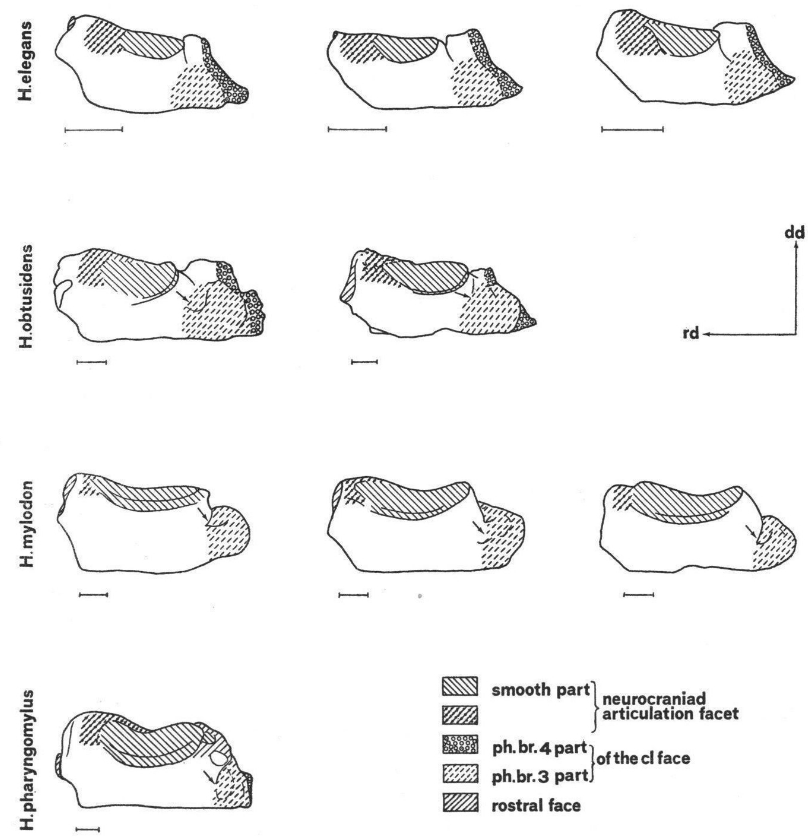


Fig. 48. Right pharyngobranchial 3,4. Medial view. Arrows point to the gutter-like impression discussed in the text (pp 250, 252). Scale = 1 mm.

b. *Borders of the neurocraniad articulation facet* (Fig. 47). In *H. elegans* the borders of the neurocraniad articulation facets run more or less straight, but in *H. mylodon* and *H. pharyngomylus* the lateral border of the neurocraniad articulation facet is incurved mediad and the medial border is excurved mediad. In *H. obtusidens* the lateral border is incurved mediad and the caudal half of the medial border is excurved mediad but the rostral half is incurved laterad.

c. *Margin between the neurocraniad articulation facet and the medial face* (Figs 47, 48). In *H. mylodon* and *H. pharyngomylus* the margin between the neurocraniad articulation facet and the medial face is

sharp. The medial border of the neurocraniad articulation facet forms a rim-like elevation, a thick rounded border above the medial face. In *H. obtusidens* the sharp margin between neurocraniad articulation facet and medial face and the rim-like elevation are only present in the caudal half of the border. In specimen W-025-001 these features were more developed than in specimen W-025-003. In *H. elegans* traces of a rim on the caudal quarter of the border were detectable in only two out of five specimens and the margin between the neurocraniad articulation facet and the medial face is less sharp, the rostral half is smoothly excurved.

d. *Length of the smooth part of the neurocraniad articulation facet* (Fig. 47, Table II: t,n,s, s/t, s/n). As compared with *H. elegans* the relative length of the smooth part in *H. mylodon* is greater with regard to the total length of pharyngobranchial 3,4. This is attributable to two mutually enhancing factors:
   1. Proportionally the smooth part occupies a relative larger part of the dorsal surface of the neurocraniad apophysis.
   2. The length of the neurocraniad apophysis is greater in *H. mylodon*, see before. In *H. obtusidens* the ratio of the smooth part to the neurocraniad articulation facet is like that of *H. elegans*. Although this ratio is the same for *H. pharyngomylus* and for *H. elegans*, the smooth part in *H. pharyngomylus* is nearly as extensive as in *H. mylodon*, on account of the long neurocraniad articulation facet.

e. *Ventrad incurvation of the neurocraniad apophysis* (Fig. 48, Table II: r, c, d, c/r, d/r). In medial view it appears that the neurocraniad apophysis of *H. mylodon* and *H. pharyngomylus* is incurved ventrad, the lowest point lies in the middle. In *H. elegans* the rostral point of the neurocraniad apophysis is the highest and the caudal point the lowest. *H. obtusidens* is, in this aspect, more like *H. mylodon*, the neurocraniad apophysis being somewhat incurved ventrad.

f. *Direction of the medial face*. In the series *H. elegans*, *H. obtusidens*, *H. mylodon*, *H. pharyngomylus* the facing vector of the medial face changes from dorso-mediad to ventro-mediad. In dorsal view the medial face of the pharyngobranchia 13,4 of *H. elegans* is visible, while it is not in the other three species (Fig. 47).

g. *Transverse crest*. The dorsal border of the transverse crest is sharp in *H. elegans*, and rounded in the other species.

3. *Differences between the pharyngobranchial 3 part of the caudal faces*. In the series *H. elegans*, *H. obtusidens*, *H. mylodon* the pharyngobranchial 3 part of the caudal face becomes bulbous. In *H. elegans* it is a rather steep and slightly convex, dorso-caudad facing declivity. At the caudal

TABLE II

Measurements taken in tracing trophically correlated shape differences in the pharyngobranchial 3,4 of intrapharyngeal mollusc-crushing species and *H. elegans*.

Species and specimen nr.	*Side*	*Length measurements in mm*				%	%	%	%	°	°	°	*Length measurements in mm*			%	%
		t	p	n	s	n/t	n/p	s/n	s/t	α	β	γ	r	c	d	c/r	d/r
H. elegans																	
W-006-131	left	2,9*	2,7	1,6	1,2	56*	58	73	41*	63	140	± 118	1,2	1,1	1,1	87	87
W-006-132	right	3,2	2,9	1,8	1,2	57	63	64	36	59	137	± 121	1,5	1,2	1,2	80	80
W-006-133	right	3,1	2,8	1,7	1,2	55	61	69	38	62	138	± 124	1,3	1,2	1,2	92	92
W-006-134	left	2,9	2,6	1,5	1,0	50	58	69	35	59	130	± 120	1,3	1,2	1,2	94	94
W-006-136	right	3,0	2,7	1,8	1,1	59	65	65	38	60	133	± 126	1,7	1,3	1,3	81	81
H. obtusidens																	
W-025-003	right	7,0*	6,7	3,8	2,8	54*	56	74	40*	57	134	± 114	3,3	2,8	2,7	87	85
W-025-001	right	7,5	7,1	4,7	3,0	63	66	63	39	64	136	± 108	3,5	3,1	3,0	87	84
H. mylodon																	
W-016-002	right	6,5	6,5	4,5	4,2	69	69	93	65	65	125	± 91	3,1	2,9	2,6	95	85
W-016-017	right	6,9	6,9	4,8	4,0	69	69	83	58	71	118	± 96	3,4	3,3	2,9	94	84
W-016-018	right	7,0	7,0	4,8	4,3	69	69	90	62	71	116	± 98	3,6	3,2	3,1	87	85
H. pharyngomylus																	
W-041-001	right	8,1	8,1	7,2	4,5–5,2	89	89	62–72	56–64	75	110	± 98	4,4	3,9	3,6	89	81

* Lateral-caudal part damaged, figures of actual total lengths slightly underestimate total length of intact preparation.

foot of the rostral-medial eminence a shallow, gutter-like impression is found in *H. mylodon* (Figs 47, 48; arrows indicate gutter). The form of the pharyngobranchial 3 part of the caudal face of *H. obtusidens* is intermediate between that of *H. elegans* and that of *H. mylodon*, the gutter-like impression is very shallow and wide. In *H. pharyngomylus* the gutter-like impression is conspicuous, but the bullate aspect of the caudal face is less prominent than in *H. mylodon*.

4. *Direction of the rostral face*. In *H. elegans* the rostral face is overhanging with regard to the rostral limit of the dentigerous area. In *H. mylodon* and *H. pharyngomylus* the rostral face is perpendicular to the dentigerous area. In *H. obtusidens* (W-025-003) the rostral face is over-

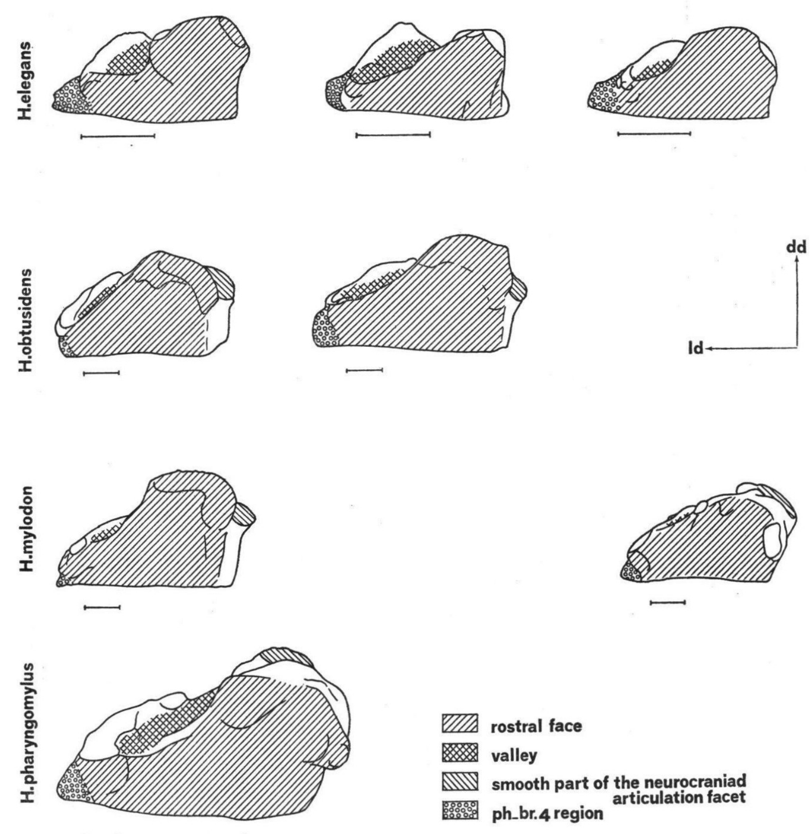


Fig. 49. Right pharyngobranchial 3,4. Rostral view. Scale = 1 mm.

hanging like in *H. elegans*, whereas in specimen (W-025-001) it is more like *H. mylodon*.

5. *Height of the caudal-lateral eminence* (Figs 48, 49). In the series *H. elegans*, *H. obtusidens*, *H. mylodon* the height of the caudal-lateral eminence decreases. In *H. elegans* it is as high as, or higher than the caudal part of the neurocraniad apophysis. In *H. obtusidens* the caudal-lateral eminence is nearly as high as the caudal part of the neurocraniad apophysis but not so much elevated above the valley as in *H. elegans*. In *H. mylodon* and *H. pharyngomylus* it is much lower than the neurocraniad apophysis. In the three molluscivorous species the epibranchiad 3 and 4 facets on the caudal-lateral eminence are also somewhat more dorsal facing than in *H. elegans*.

6. *Height and facing of the valley*. As compared to *H. elegans*, the valley (including the valley recess) and the pass are shallow in the molluscivorous species. The shallowness of the valley is explained partly by a relative dorsad elevation of the valley and partly by the relative low caudal-lateral eminence.

Conclusion

Though there are intraspecific variations, pharyngobranchial 3, 4 of the molluscivorous species always differs trenchantly from that of the insectivorous species in the above mentioned properties. For many of these properties a functional interpretation is given in WITTE & BAREL (1976). Concerning the quantitative aspects of the various shape features of pharyngobranchial 3,4, the values generally decrease or increase in the series: *H. elegans*, *H. obtusidens*, *H. mylodon* and *H. pharyngomylus*. *H. pharyngomylus* often occupies a relatively extreme position.

The palatine region in paedophagous species (Figs 50–51, Table III)

Definition of measurements (Fig. 50)

The quantitative comparison of the shapes of the palatine region is based on the following measurements.

1. *Angles and lengths in the rostral border* (Fig. 51: AB, BC, CD). The rostral border can be divided into a dorsal part (AB), a middle part (BC) and a ventral part (CD). Through these more or less straight parts three lines are drawn. The rostral angles between the lines are defined as the angles between the parts.

2. *Caudal palatine depth* (Fig. 50, dc). The caudal palatine depth is the shortest distance from the rostral border to the caudal-dorsal border

of the palatine region, measured perpendicular to the middle part of the rostral border.

3. *Heigth of the mesethmoidal process* (Fig. 50, h). The height of the mesethmoidad process is the distance from the line connecting the highest points of the rostral saddle to the deepest point, measured in medial view.

4. *Wing extension* (Fig. 50, w). The wing extension is the greatest width of the palatine region, in ventral view.

5. *Facet distance* (Fig. 50, t). The facet distance is the greatest distance between the mesethmoidad process and the palatine wing, in medial view.

6. *Vertical depth* (Fig. 50, d). The vertical depth is the shortest distance between the caudal saddle and the ventral border of the palatine region caudal to the wing, measured in medial view.

7. *Palatine length* (Fig. 50, pl). The palatine length is the distance from the maxillad articulation facet to the most caudal point of the lateroethmoidad articulation facet.

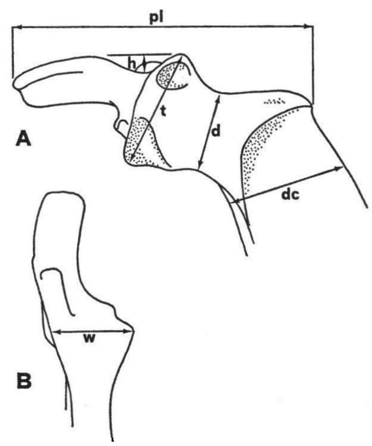


Fig. 50. Palatine region of the suspensorium. Measurements taken in studying trophically correlated shape differences in paedophagous species and *H. elegans*. A: medial view. B: ventral view. The measurements are defined in the text on pp. 253–254.

Shape-differences (Figs 51–53; Table III)

For the palatine region the shape-differences between *H. elegans* and paedophagous species may be summarized as follows:

1. *The rostral border* (Fig. 51)

a. In *H. elegans* the rostral border can be divided into a dorsal hori-

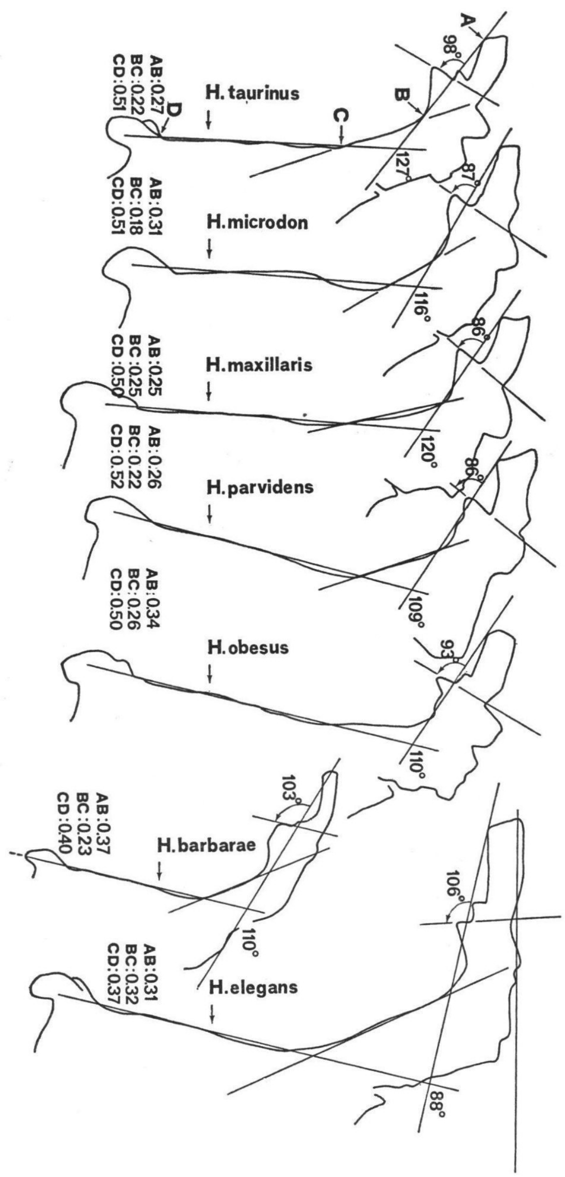


Fig. 51. Palatine region of the suspensorium. Left side. Lateral view. AB, BC and CD are parts of the rostral border, discussed in the text on pp. 253, 254, 256. The relative lengths of these parts with regard to the total length of the rostral border are indicated at the bottom of each figure.

zontal part, a rostrad-dorsad middle part and a ventral vertical part. These parts are of almost the same length. However, in paedophages the sum of the lengths of the two upper parts is approximately the same as the length of the ventral vertical part. The shorter middle part is rostro-dorsad directed whereas the dorsal part is dorso-rostrad directed. The angle formed between the lines produced by the dorsal and ventral part varies in *H. elegans* between 78° and 102°. In the paedophages it varies between 109° and 127°.

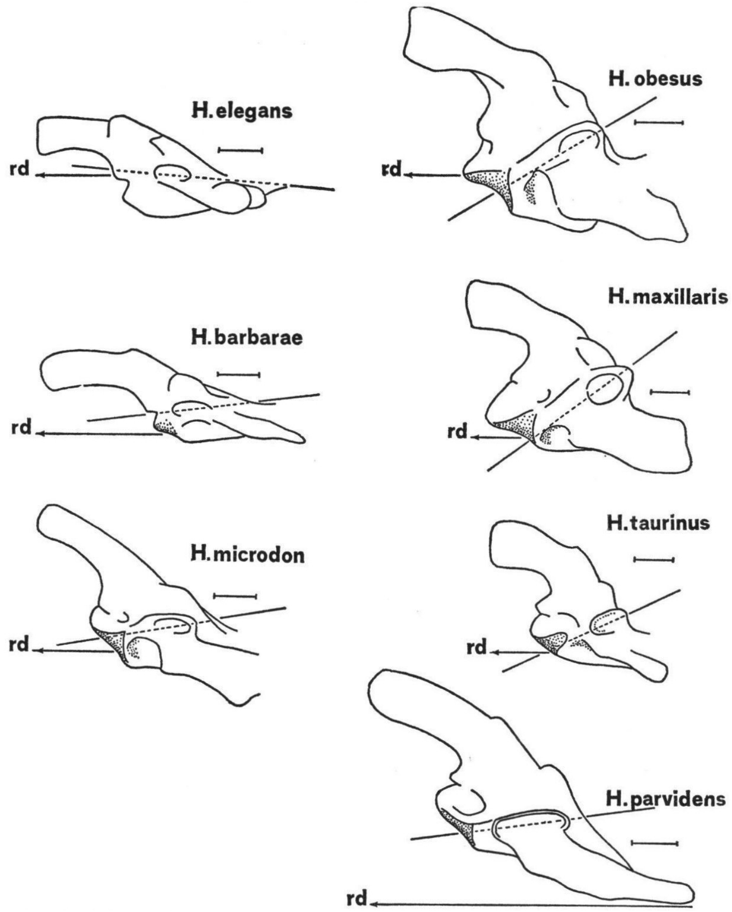


Fig. 52. Palatine region of the suspensorium. Dorsal view. Right side, except for *H. taurinus* and *H. parvidens* which are mirror-images of the left side. The dotted lines mark the directions of corresponding parts of the vomerad articulation facets. Scale = 1 mm.

b. *Thickening of the rostral border.* In the paedophages the rostral suspensorial border is thickened over its whole length, especially near the mandibulad articulation facet and the dorsal section of the middle part.

c. *Caudal palatine depth* (Fig. 53, Table III). The caudal palatine depth is greater in the paedophages as compared to *H. elegans.*

2. *The direction of the palatine region* (Fig. 52). In the paedophages the part of the palatine region that lies dorsal to a horizontal line through the corner formed by the dorsal and the middle part of the rostral suspensorial border is, as a whole, extending away from the main suspensorial plane in a laterad direction.

3. *The palatine fossa.* A medial view reveals that, in the paedophages, the palatine fossa is either inconspicuous or completely lacking. In the former case the fossa ledge is not raised as in *H. elegans* but is merely present as a rim. The fossa dome is absent in the paedophages. In the paedophages the lateral wall of the fossa gradually merges into the dorsal-caudal part of the medial face of the palatine region.

4. *Articulation facets and related shapes* (Figs 51, 52, 53, Table III). In the paedophages both the wing and the mesethmoidad process extend much more distad respectively from the ventral and dorsal border of he maxillad process than in *H. elegans.* Concomitant with the greater vertical depth of the mesethmoidad process, both rostral and caudal saddle are deeper in the paedophages. The angle between the rostral border of the vomerad articulation facet and the ventral border of the maxillad process is more acute in the paedophages. As a result the vomerad articulation facet and the mesethmoidad articulation facet lie farther apart which gives the paedophagous palatine region its typical "winged" appearance.

The mesethmoidad facet which is mediad facing in *H. elegans,* is caudo-mediad facing in the paedophages.

In the paedophages the rostral border of the vomerad articulation facet gradually merges into the dorsal corner of the mesethmoidad articulation facet thus connecting the two facets by means of a ridge (the *interfacet ridge).* Rostrad this ridge slopes downwards to the maxillad process. Caudal to this ridge and dorso-caudal to the mesoethmoidad articulation facet lies a pit. In *H. taurinus* the distance between the vomerad articulation facet and the mesoethmoidad articulation facet is not entirely occupied by the interfacet ridge. Owing to this, part of the rostral limitation of the pit is lacking. *H. taurinus,* however, does have a distinct pit compared to *H. elegans,* where neither pit nor any trace of an interfacet ridge are present.

TABLE III

Measurements taken in tracing trophically correlated shape differences in the palatine region of paedophagous species and *H. elegans*.

Species	*Specimen number*	*Side*	*pl*	*d*	*h*	*w*	*t*	*dc*	*pl/d*	*pl/h*	*pl/w*	*pl/t*	*pl/dc*
H. taurinus	W-004-009	R	6.41	2.32	0.83	2.16	2.28	1.83	2.64	7.40	2.85	2.18	3.36
	W-004-009	L	6.41	2.32	0.83	2.16	2.28	1.83	2.64	7.40	2.85	2.18	3.36
	W-004-008	L	6.64	2.32	1.16	2.49	3.49	1.99	2.86	5.17	2.61	1.90	3.33
H. microdon	W-037-002	R	8.30	2.99	1.16	2.66	4.15	2.32	2.78	7.14	3.81	2.00	3.13
	W-037-002	L	8.30	2.99	1.16	2.66	4.15	2.66	2.78	7.14	3.81	2.00	3.57
H. maxillaris	W-029-004	L	8.80	3.32	1.00	3.49	4.65	2.82	2.65	8.83	2.52	1.89	3.12
	W-029-004	R	8.80	3.32	1.16	3.98	4.98	2.66	2.65	7.57	2.21	1.77	3.31
	W-029-003	L	9.79	3.49	1.16	3.82	4.98	2.99	2.81	8.43	1.84	1.97	3.28
	W-029-003	R	9.79	3.49	1.00	3.98	5.15	2.82	2.81	9.83	2.46	1.90	3.47
H. obesus	W-027-004	R	9.30	3.15	1.16	3.32	4.48	3.15	2.95	8.00	2.80	2.01	2.95
	W-027-004	L	9.30	2.99	1.00	3.32	4.65	3.32	3.11	9.33	2.80	2.00	2.80
	W-027-003	R	10.13	3.15	1.16	3.98	4.98	3.65	3.21	8.17	2.55	2.03	2.77
H. parvidens	W-032-003	L	11.79	4.98	0.83	3.32	4.65	3.32	2.31	14.20	3.55	2.54	3.55
H. barbarae	W-043-002	R	7.80	1.99	0.33	1.99	2.66	1.83	3.75	23.50	3.75	2.93	4.63
H. elegans	W-006-133	R	4.15	1.16	0.33	—	—	—	3.64	12.50	—	—	—
	W-006-131	R	4.32	1.16	0.33	1.49	1.99	1.36	3.71	13.00	2.98	2.17	3.71
	W-006-091	R	4.98	1.49	—	—	—	—	3.33	—	—	—	—
	W-006-111	L	4.98	1.49	0.50	1.33	1.83	1.00	3.33	10.00	3.75	2.73	5.00
	W-006-111	R	4.98	1.32	0.50	1.33	1.99	1.16	3.75	10.00	3.75	2.50	4.29
	P-006-122	R	6.64	1.83	0.66	2.32	2.99	1.66	3.64	10.00	2.86	2.22	4.00
	P-006-112	R	6.81	1.99	0.83	2.32	3.32	1.83	3.42	8.20	2.93	2.05	3.73
	P-006-108	L	7.00	1.83	0.66	2.16	2.99	1.66	3.82	10.50	3.23	2.33	4.20

measurements in mm.

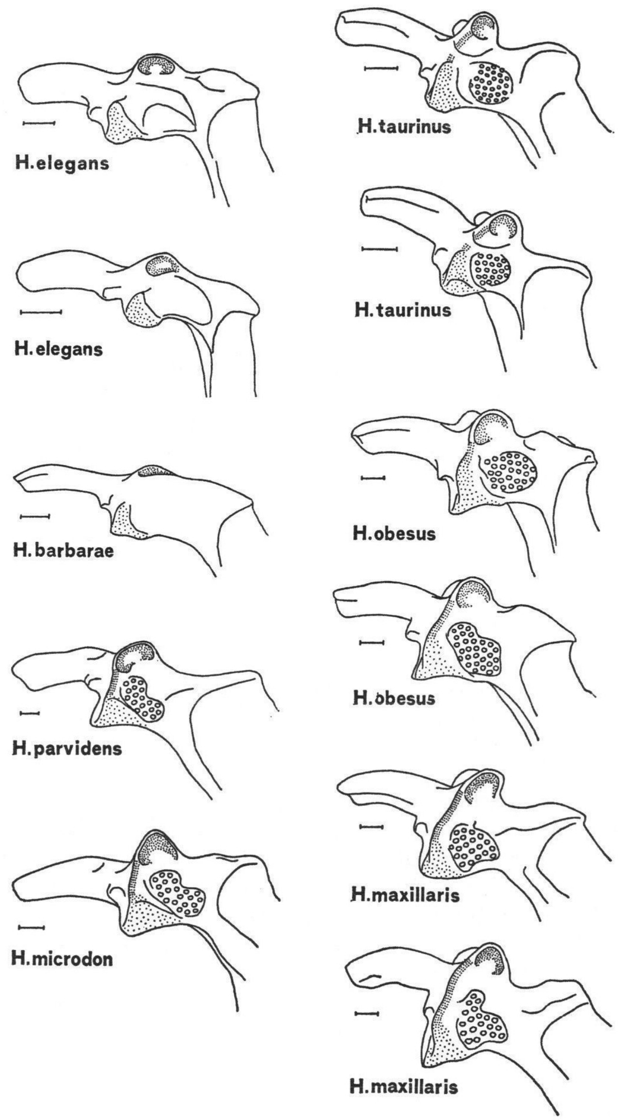


Fig. 53. Palatine region of the suspensorium. Medial view. Right side, except for *H. parvidens*, *H. microdon*, *H. taurinus* and *H. obesus* (top) which are mirror-images of the left side. The finely dotted part ventrally, marks the vomerad articulation facet, dorsally it locates the mesethmoidad articulation facet. Open circles indicate the pit. The dotted streak between the rostral borders of the two articulation facets is the interfacet ridge. Scale = 0.7 mm.

The vertical depth of the palatine region between the vomerad articulation facet and the mesethmoidad articulation facet is greater in the paedophages.

The angle between the line, connecting the centres of the vomerad and mesethmoidad articulation facets, and the vertical line is smaller in paedophages. The whole area caudal to the vomerad and the lateroethmoidad articulation facets has a greater mediad component in the paedophages.

Conclusion

On the basis of its stomach contents (recently fertilized ova), GREENWOOD (1967) includes *H. barbarae* in the group of paedophagous species but none of the anatomical features which he describes for his other paedophagous species, was observed in *H. barbarae* by GREENWOOD. On the basis of its gross anatomy GREENWOOD (1967) defines *H. barbarae* as a generalized species which accords well with our observations on the palatine region of this species. None of the features characterizing the paedophagous palatine region was observed in *H. barbarae*. In fact the shape of its palatine region was closer to this region in *H. elegans*.

In contradistinction to *H. barbarae*, *H. microdon* was included in the paedophages solely because of its gross anatomy. Nothing is known about its food (GREENWOOD, 1959). The anatomical paedophagous features which GREENWOOD lists for *H. microdon*, can be amplified by our observations on its palatine region which exhibits all the features observed for the well-established paedophagous species.

Except for *H. barbarae*, the paedophages can be distinguished from *H. elegans* on the basis of a number of shape differences in the palatine region and the rostral border of the suspensorium. FRYER & ILES (1972: 101) state that "Although this specialized feeding behaviour (*the paedophagous feeding habbits*, our italics) is common to several species it is not accompanied by marked convergence in head or jaw structure..." and "The lack of striking diagnostic indications of feeding habits among these fishes ...". From our observations we would conclude that there are such diagnostic characters, at least in the above mentioned zones. The functional morphological significance of those characteristic features are, as yet, unknown but they seem to point to one mechanism underlying the paedophagous habit.

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TABLE OF PREPARATIONS

SOURCE: Kind of preparation on which the figure is based. SL: standard length of the intact specimen from which the preparation has been obtained.
SPECM. NR. Individual number of the specimen from which the preparation has been obtained. "W" indicates a specimen caught in a lake and preserved immediately after being caught; "P" a specimen which was caught in a lake and kept in tanks for a certain period; "F_1" the first generation bred in tanks.
Skel.: Dry skeletal element. *Preserved:* intact preserved specimen.
Aliz.: preparation in which bone has been stained with Alizarin red.
Aliz. Alc.: Preparation in which bone has been stained with Alizarin red and cartilage with Alcian blue. *Scan:* gold-coated preparations from macerated skeletal elements. Figures from these preparations are based on stereoscan-photographs from the preparations, completed with observations of the preparations.
Gold-coated: gold-coated preparations of the larger skeletal elements.
S-Sections: sections of elements from serial sections of a complete head.
Rec.: Reconstruction from serial sections following the technique described by ANKER (1974).

Fig.	*Source*	*SL (mm)*	*Specm. nr.*
1A	preserved	69	W-006-144
1B	preserved	99	F_1-006-143
2	preserved	69	W-006-144
3	—	—	—
4A	Aliz. Alc.	70	W-006-091
4B	Aliz. Alc.	73,5	W-006-093
5	Aliz. Alc.	70	W-006-091
7	Aliz. Alc.	104	P-006-100
	S-Sections	67	W-006-007
8	Aliz.	—	W-006-001
9A	Scan	68	W-006-111
9B	Scan	63	W-006-136
10	Scan	95	P-006-112
11	Scan	68,5	W-006-094
12A	Scan	68	W-006-111
12B	Scan	68	W-006-111
13	fig. 14		—
14A	gold-coated	93	P-006-122
14B	S-Sections	67	W-006-007
15	Scan	61	W-006-131
16A	fig. 15		—
16B	S-Sections	67	W-006-007
17	Scan	95	P-006-112
18	Skel.	61	W-006-131
19A	Scan	95	P-006-112
20	Skel.	61,5	W-006-132
21A	Scan	68	W-006-111
21B	fig. 21A		—
21C	Scan	63	W-006-136
21D	fig. 21C		—
21E, F	S-Sections	67	W-006-007

Fig.	*Source*	*SL (mm)*	*Specm. nr.*
22	Scan	68	W-006-111
23A	Skel.	101,5	P-006-103
23B	Scan	108	P-006-108
23C	Scan	95	P-006-112
24A, B	Scan	68	W-006-111
24C	fig. 24A		
25A, B	Scan	108	P-006-108
26A, B, C	Scan	63	W-006-136
27A, B	Scan	103	P-006-109
28A, B	Scan	103	P-006-109
29A, B	Scan	95	P-006-112
30	Scan	95	P-006-112
31A	Scan	61,5	W-006-132
31B	Scan	56	W-006-134
32A, B, C	Scan	103	P-006-109
33A	Scan	95	P-006-112
33B	Scan	68	W-006-111
34A	Scan	95	P-006-112
34B, C	Scan	108	P-006-108
35A	Aliz. Alc.	70	W-006-091
35B	Scan	68	W-006-111
	Scan	69	W-006-094
	Scan	68	W-006-111
36A	Scan	103	P-006-109
36B	Scan	95	P-006-112
37	Reconstr.	67	W-006-007
38	Reconstr. + S-Sect.	66,5	W-006-036
39	Scan	95	P-006-112
40	Scan	61,5	W-006-132
41	Scan	95	P-006-112
42	Scan	95	P-006-112
43	Scan	95	P-006-112
44	Scan	93	P-006-123
45A	Scan	108	P-006-108
45B	Scan	93	P-006-123
46A	Skel.	61,5	W-006-132
46B	Skel.	61,5	W-006-132
46C	Scan	89,5	W-016-017
47, 48A, B			
H. elegans left	Skel.	61,5	W-006-136
H. elegans middle	Skel.	60	W-006-133
H. elegans right	Skel.	63	W-006-132
H. obtusidens left	Skel.	—	W-025-003
H. obtusidens right	Skel.	103	W-025-001
H. mylodon left	Skel.	90	W-016-018
H. mylodon middle	Scan	89,5	W-016-017
H. mylodon right	Skel.	79	W-016-002
H. pharyngomylus	Skel.	106	W-041-001

Fig.	*Source*	*SL (mm)*	*Specm. nr.*
51			
H. taurinus	Skel.	121	W-004-008
H. microdon	Skel.	120	W-037-002
H. maxillaris	Skel.	—	W-029-003
H. parvidens	Skel.	133	W-032-003
H. obesus	Skel.	—	W-027-003
H. barbarae	Skel.	—	W-043-002
H. elegans	Skel.	60	W-006-132
52			
H. obesus	Skel.	—	W-027-003
H. maxillaris	Skel.	—	W-029-004
H. taurinus	Skel.	121	W-004-008
H. parvidens	Skel.	133	W-032-003
H. elegans	Skel.	93	P-006-122
H. barbarae	Skel.	—	W-043-002
H. microdon	Skel.	120	W-037-002
53			
H. taurinus top	Skel.	121	W-004-008
H. taurinus lower	Skel.	82	W-004-009
H. obesus top	Skel.	119	W-027-004
H. obesus lower	Skel.	—	W-027-003
H. maxillaris top	Skel.	—	W-029-003
H. maxillaris lower	Skel.	—	W-029-004
H. elegans top	Skel.	93	P-006-122
H. elegans lower	Skel.	68	W-006-111
H. barbarae	Skel.	—	W-043-002
H. parvidens	Skel.	133	W-032-003
H. microdon	Skel.	120	W-037-002
IA	gold-coated	93	P-006-123
IB	IA		
IC	S-Sect.	67	W-006-007
IIA	gold-coated	93	P-006-122
IIB	Scan	68	W-006-111
III	Scan	103	P-006-109
IV	Skel.	68	W-006-005
		62,5	W-006-003
VA	Scan	68	W-006-111
VB	Scan	62,5	W-006-003